HORN FLY BREEDING, NITROGEN LOSS AND NUTRIENT IMMOBILIZATION ASSOCIATED WITH CATTLE DUNG IN THE SOUTHERN INTERIOR OF BRITISH COLUMBIA

by

ANGUS MACQUEEN

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Name: Angus Macqueen

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Examining Committee:

Chairman: Dr. A. L. Turnbull

B. P. Beirne
Senior Supervisor

R. C. Brooke

J. P. M. Mackauer

R. M. F. S. Sadleir

W. G. Wellington
External Examiner
Professor of Plant Science
and Resource Ecology
University of British Columbia

Date Approved: May 16, 1973.

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Horn fly breeding, nitrogen loss and nutrient immobilization associated with cattle dung in the southern interior of British Columbia.

Author:

(signature)

Angus MacQueen

(name)

16th August 1973.

(date)

ABSTRACT

Cattle dung and some associated insects cause problems in the rangelands of the Southern Interior of British Columbia. Three of these problems were investigated: (i) the production of a pest species, the horn fly, Haematobia irritans (Linnaeus), which breeds in fresh dung; (ii) nitrogen loss from dung; and (iii) immobilization of potential plant nutrients in undecomposed dung pads. These problems are intensified by the lack of an effective coprophagous beetle fauna in the area.

The field research was done at Kamloops, British Columbia, during 1971 and 1972. Horn fly production from dung was measured in the presence and absence of other insects. Adult female flies were trapped at dung pads after oviposition during the day and at night. The pads were then either exposed to field insects for 24 hours or covered with frames excluding insects for the same period, after which they were removed to a greenhouse where all fauna emerged. The number of adult horn fly progeny produced per ovipositing female was obtained for each pad. The effect of other insects on horn fly was measured by comparing the progeny produced per female for both exposed and covered pads that were deposited about the same time.

Horn fly females did not show a definite diurnal rhythm in oviposition. Numbers of progeny produced per female fly showed an apparent peak from 0300-0600, while lowest numbers were produced in the early evening. Approximately half the common insect species in cattle dung at Kamloops are known or thought to be exotic. The overall effect of these insects was to suppress horn fly production from dung pads mainly by predation.

Nitrogen (N) loss from dung was measured by exposing dishes of fresh feces outdoors in a screened cage. House fly larvae (Musca domestica Linnaeus) were used to measure the contribution of coprophagous Diptera to this loss. Little N was lost from pads when insects were absent. Nitrogen loss from artificial 960-g dung pads exposed to other insects in the field did not exceed 13.5% after 16 days. Nitrogen content of dung 10 days after being seeded with increasing numbers of fly larvae bore an inverse relationship to the original number of larvae used. Heavy infestations of dipterous larvae caused the loss of more N than was removed in insect tissues. Volatilization of ammonia by microorganisms together with excretion of ammonia by larvae may be responsible for this.

Only two species of dung-burying beetles are present at Kamloops. The dung burial efficiency of Onthophagus nuchicornis (Linnaeus), originally introduced accidentally, was measured in greenhouse experiments. This species was also used to assess the effect of dung burial on the development of fly larvae and on the growth of range grass. When fly larvae were present in dung at certain densities, their survival was inversely related to the number of brood balls constructed by the beetles. Beetles do not bury dung in midsummer, which is the time of greatest horn fly activity in the field, and they do not have any useful effect in removing dung from pastures.

The nutrient value of fresh dung for range plants was evaluated over two seasons in a pot experiment using depleted range soil and beardless wheatgrass, Agropyron spicatum (Pursh) Scribn. & Smith. Dung treatments included one in which 200 g of fresh feces were fully mixed with the pot soil (330 lb/acre N) and another where a portion of the same quantity of dung was buried in the soil by O. nuchicornis (120 lb/acre N). Total

incorporation of the fresh dung into the soil increased the total crude protein production of the wheatgrass over that of the untreated control by 100% over two years, and also increased the potential seed production and vigor of the grass. Burial of an average of 37% of the available dung by beetles caused a 38% increase in crude protein over that of the control during the same period.

The nature of problems caused by cattle dung in British Columbia suggests that introduction of additional species of exotic dung beetles should be considered. The original nutrient cycles were altered when cattle were introduced into British Columbia and allowed to overgraze range pastures without introduction of any Old World insects that are specialized in the removal of their dung. Addition of efficient cattle dung beetles should furnish a useful ecological component that has hitherto been absent from this pastoral system.

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GENERAL INTRODUCTION

The Problems.

Cattle dung does not decompose quickly in the semi-arid rangelands of the Southern Interior of British Columbia. Dried dung pads remain on the soil surface for long periods of time, possibly for years in some situations. The continuing addition of cattle dung to the pastoral system in this area appears to have created problems basically similar to those that occur in Australia, and which were documented by Bornemissza (1960), Gillard (1967), and Bornemissza and Williams (1970):

- utilization of fresh dung pads as a food medium by larvae of some pest flies;
- slow nutrient turnover with substantial losses of nitrogen from dung pads;
- the cluttering of rangeland and pastures with dry dung pads that reduce grazing area and at the same time cause rank grass growth around their perimeter that is usually rejected by cattle;
- encouragement of weed growth.

In British Columbia, the most noticeable problems are the breeding of two fly pests of cattle (the horn fly, Haematobia irritans (Linnaeus) and the face fly, Musca autumnalis DeGeer) in fresh dung, the cluttering of pasture land with dry dung pads, and the patches of rank grass growth that appear in the vicinity of pads deposited in moister situations.

Coprophagous Insects.

One group of insects that is both economically and ecologically important utilizes animal excrement. The dung of vertebrates, particularly that of the larger mammals, provides a source of food for many insects. Some of these are pests of domestic animals and man; others play an active role in dung removal and decomposition. Insect larvae, adults or both stages may depend directly upon feces for their food. These coprophagous forms may be attacked by parasites and predators which thus depend indirectly upon the feces for their nourishment.

Of all animals, insects have been the most successful in exploiting this biotope. They are represented primarily by certain families within the orders Coleoptera, Diptera and Hymenoptera, and in some warmer areas of the world, also by Isoptera (Ferrar and Watson, 1970). The Coleoptera and Diptera include both coprophagous and entomophagous species. The Hymenoptera are represented only by entomophagous species, while the Isoptera are coprophagous but feed on older dung after it has mostly dried out and the majority of other species have departed.

Most insect activity, feeding and interactions occur in relatively fresh dung within a week or two after it has been deposited. During this time the dung changes quite rapidly in its physical, chemical and presumably microbiological characteristics. Fresh dung with its high moisture and nutrient content is utilized by a wide range of coprophagous insects, whereas the same dung mass when air-dried supports a much smaller number of species.

Coprophagous insects may be divided arbitrarily into two categories on the basis of their feeding habits. In the first category belong certain dipterous and coleopterous larvae and adults that feed on the dung in situ, utilizing some of the nutrients but leaving the dung mass apparently

undisturbed except for tunnels in the interior. These forms I term "passenger" species because their activity results in a net export of nutrients from the pad in the form of insect tissue with little or no direct incorporation of dung into the underlying soil.

In the second category are those insects which physically manipulate the dung mass as part of their feeding or reproductive behavior. The Scarabaeinae and some Geotrupinae of the coleopterous family Scarabaeidae are renowned for this type of activity. They are commonly known as dung beetles.

Dung beetles play an extremely important role in the biological cycle of the biomes to which they belong (Halffter and Matthews, 1966). Their general habit of burying dung in the soil to provision themselves and their larvae leads to removal of quantities of excrement from the soil surface. When the dung is buried in the soil, it is placed in close contact with other decomposer organisms and thus breakdown and recycling of dung nutrients may occur quite rapidly. Some of the buried dung is used to produce insect (i.e., beetle) tissue but there is also an appreciable return of nutrients to the soil.

Coprophagous Aphodiinae (Scarabaeidae), though often referred to as "dung beetles", do not bury dung after the fashion of the Scarabaeinae and Geotrupinae mentioned above. Aphodiine beetles when present in large numbers in dung masses may fragment and disperse them, and in this way speed up the decomposition process.

Some dung beetle species are attracted only to dung of particular animal species while a larger number feed indiscriminately, or with a low degree of preference, on the various types of dung available or even on cadavers or decaying fruits (Halffter and Matthews, 1966). The variety and

abundance of dung beetle species in any area is directly correlated with that of the native mammalian fauna (Bornemissza, 1960).

There also appears to be a marked degree of specialization in regard to the form of dung utilized. Beetles that can dispose of pellet-type dung are generally unable to utilize any dung which is in the form of a pad, while those adapted to pads may find dung pellets totally unsuitable. This was clearly demonstrated in Australia (Bornemissza, 1960), where indigenous herbivores that produce a pad-type dropping are lacking though an abundant marsupial fauna is present. The herbivorous marsupials produce pellet-type droppings and the Australian native dung beetle fauna is adapted to utilize these. Consequently cattle dung is not used by the indigenous beetles to any extent, although many of the species may be attracted to it.

The Spread of Domestic Cattle.

In Europe, the area of origin of the domestic bovid Bos taurus Linnaeus (Darlington, 1957; Walker, 1968), there is an extensive beetle fauna adapted to deal with this and other types of dung. Moreover, especially in the warmer parts of the world, it is apparent that each area of origin for a particular bovine species has dung beetles which evolved with it and are specialized in the removal of its dung at certain times of the year (Bornemissza, 1960; Halffter and Matthews, 1966).

Man has been responsible for introducing Bos taurus into all continents and most islands of the world and more recently Bos indicus Linnaeus (Brahman cattle) and Bubalus bubalis (Linnaeus) (Asian water buffalo) have been established in new areas. In every case the animals were introduced without any conscious effort to import the dung-burying beetles that attended to their feces in their native country, because at the time of introduction the significance

of these beetles was not appreciated. If new cattle species are introduced into areas that already have other large indigenous Bovidae (e.g., Africa, Asia) then native beetles may dispose of the additional dung. Where large indigenous bovids have never been present there is no chance of true pad-utilizing beetles having evolved, so that dung of exotic bovids would remain mostly unburied.

The large bovid Bison bison (Linnaeus), the only indigenous animal that produces a dung pad superficially very similar to that of cattle, once ranged over most of North America except the northeast portion above the Great Lakes (Roe, 1970). Its territory thus extended from the plains and some woodlands of Canada to the Mexican plateau, and from the inner edge of Oregon at least to western New York and Georgia (Darlington, 1957). However, recent bison did not reach the coastal Pacific Northwest. There is so far only one recorded discovery of fossil bison bones in British Columbia, in Pleistocene strata at Kelowna (Roe, 1970). Osborne (1953) showed that at least small numbers of bison were present in eastern Washington during prehistoric and very early historic times, but there is no evidence that these recently ranged north over the International Boundary into the Southern Interior of the Province. Bison once lived in the extreme northern portions of British Columbia (Cowan and Guiget, 1965) but again their range was restricted to this area. Certainly the Interior of the Province has seen no recent bison for a long and indeterminate length of time, if ever. Hence the introduction of cattle into this area meant the arrival of not only an exotic animal but also quantities of pad-type dung.

Animal excreta serves as a source of nutrients that may be exploited by insects in various ways. Insects have had ample opportunity for evolution of forms that can utilize cattle dung in Europe, so that now

relative stability can be expected there in the species occupying the diverse niches provided by the dung. This does not preclude further speciation amongst the fauna already present, given sufficient time without human interference, or the replacement of species by more successful ecologically homologous species which are fortuitously introduced from other areas.

In contrast, cattle dung in an area that previously supported no native cattle, and consequently had no insect fauna specifically adapted to their dung, is available for exploitation primarily by only the opportunists amongst the native insects. The nature of the utilization will depend upon what types of opportunists are present. An insect that can utilize the new dung satisfactorily is likely to increase greatly in numbers, a situation which could prove troublesome from the human point of view if any of these has pest potential. When coprophagous cattle dung insects are accidentally introduced into this system, they generally find conditions particularly suitable for rapid multiplication, due to an abundance of food and a lack of their normal natural enemies. For example, the horn fly and the face fly, which breed in fresh cattle dung, have understandably prospered in North America after being introduced separately from Europe. A similar case is that of the buffalo fly, which in the 1820's was brought to Australia from Timor with its normal host, the Asian water buffalo (CSIRO, 1969). The adult fly then transferred its attentions to the various domestic cattle breeds, and its larvae were able to develop successfully in their dung pads.

Previous Biological Control Attempts.

The appearance of cattle dung in a new area following the introduction of these animals thus may cause problems because of the inability

of the system to cope with it. At the same time, a unique opportunity appears in each country of introduction for the deliberate selection by man of exotic insects to effect dung disposal. In the first attempt known to the writer, three species of Scarabaeinae were introduced into Puerto Rico from Texas together with one species each from Santo Domingo and Illinois, in an unsuccessful effort to control the horn fly (Wolcott, 1922, cited by Halffter and Matthews, 1966).

In 1921 three scarabaeine species from the Philippines were imported and released into Hawaii for the express purpose of competing with horn fly larvae for their food (Fullaway, 1921). These early importations appear to have been quite haphazard and on no occasion was this more evident than in the attempts before and during 1921 (Fullaway, 1921) to establish Australian dung beetles (i.e., marsupial dung feeders) on cattle dung in Hawaii. These introductions failed and then the Hawaiian authorities began a search for dung beetles in the southwestern United States. According to Fullaway, before the end of 1921 four more species of dung beetles were taken to Hawaii from California and Arizona. Shortly thereafter (1923) three species of Mexican dung beetles were introduced into parts of the Hawaiian Islands and became established with varying degrees of success (Pemberton, 1935; Howden and Cartwright, 1963; Halffter and Matthews, 1966).

Bornemissza (1960) was the first to propose such a course of action for the Australian situation. He described the prolonged presence of dung on a pasture as being something akin to the presence of a noxious weed. As with an introduced weed or animal, an exotic dung pad represents a potential food source for one or more species of specialized beetles that may be sought in other areas. Selected beetle species can be imported

without their pathogens or other natural enemies and thus have an excellent chance of colonizing a new area successfully.

The nature of the intimate association between certain insects, cattle dung, and the pastoral ecosystem means that all the problems can be related to two sources:

- the presence of certain insects that breed in dung and whose adults create a nuisance;
- the apparent absence of other insects that are capable of removing the dung from the soil surface.

If cattle dung could be buried sufficiently quickly most or all of the problems could be reduced in magnitude. Natural removal of dung could only be accomplished by introduction of efficient exotic dung beetles. To enhance the chances of a successful introduction the nature of the insect complex already associated with the dung should be assessed. Information on the most important problems should be used to predict the potential benefits that might be derived from an introduction of this type. An estimation of the possible consequences of beetle activity on the grazing system should be made in advance before any beetles are liberated.

Many regions of North America have a serious field dung disposal problem; the interior of British Columbia is only one of them. None of the actual or apparent problems associated with cattle dung in British Columbia had been defined previously, and the local dung insect fauna had not been examined.

For the investigation reported here three areas were chosen representing the most serious apparent problems involving cattle dung in the rangelands. These are the production of horn fly and face fly, the potential for dung nitrogen loss, and the nutrient deprivation of range plants caused by immobilization of elements in undecomposed cattle feces.

Objectives.

The objectives of the investigation were:-

a) To define

1) the extent of fly pest production from fresh dung and some of the relationships of these flies with other insects in dung pads;

2) the extent of nitrogen loss from dung pads as they dehydrate; and

3) the effects of dung nutrients on range vegetation.

b) To assess the effects of dung burial on

1) development of the coprophagous larvae of fly pests;

2) return of nitrogen and other nutrients to the pastoral ecosystem; and

3) growth of range vegetation.

c) From the above,

to predict some likely biotic consequences of introductions of additional dung-burying beetle species into this area.

The description of the investigation of these problems has been divided into four chapters:

Chapter I describes an assessment of the breeding of the horn fly in dung in the Southern Interior of British Columbia, identification of the other insects present in dung pads, and their effect on this fly.

Chapter II describes investigations of the performance of a European dung-burying beetle that has been in British Columbia for some years, and that was subjected to field scrutiny and used as a laboratory animal for dung burial work.

Examination of nitrogen loss from cattle dung in the Interior of British Columbia forms the material for Chapter III.

Chapter IV describes work undertaken to examine the effect of dung nutrients on range plant growth.

CHAPTER I - PEST FLY PRODUCTION AND INSECT INTERACTIONS IN THE DUNG PAD

INTRODUCTION

At the start of this investigation the role of cattle dung in producing both face fly and horn fly was considered.

The Face Fly.

The face fly is a recent immigrant in British Columbia. It is a European species that was first recorded in North America from Nova Scotia in 1952 (Vockeroth, 1953), and by 1966 had become established in the southeast portion of British Columbia, having entered from Washington across the International Boundary (Depner, 1969). In 1967 the fly was found in nearly all areas of the province south of Williams Lake (Depner, 1969) and evidently formed very heavy infestations (Creelman, 1967).

Considered to be one of the major livestock pests over much of its range in North America, the face fly attacks cattle and to a lesser extent horses (Teskey, 1969). Adult flies feed on body secretions and blood from wounds of the hosts, and the larvae require fresh cattle feces for their development. The protective and evasive actions of cattle in response to the irritation caused by feeding flies result in lost grazing time that may reduce milk flow or weight gain (Teskey, 1969).

The future pest potential for the face fly in British Columbia is not known. Its numbers were low in the Interior of the Province in 1970 through 1972 and its appearance at dung was erratic, this being a noticeable change from the heavy infestations that had been observed in previous years, particularly in 1967 and 1968 (G. B. Rich, personal communication).

Face flies collected at Kamloops in 1971 were examined for me by Mr. C. M. Jones, USDA Entomology Research Division then at the University of Nebraska, who found (in litt.) that they were very heavily infested with the parasitic nematode Heterotylenchus autumnalis Nickle. The nematode may be responsible for the decline in face fly numbers. It was considered to be a possible factor in suppressing face flies in Missouri in 1968 (Thomas and Puttler, 1970) and an important natural control agent of this species in 1970 (Thomas, Puttler, and Morgan, 1972). The face fly could not be considered a significant pest at the start of this investigation. Added to this was the impossibility of following the population processes of immature face flies and horn flies with the same field experimental technique. The face fly was therefore not investigated further, and attention was focused on the horn fly, which remains a persistent pest in the Interior of the Province.

The Horn Fly.

The horn fly is generally considered to be one of the most serious pests of cattle wherever it occurs (McLintock and Depner, 1954). Both adult sexes are haematophagous, mainly on cattle but occasionally on other domestic animals (Bruce, 1964). Adults obtain food by lacerating the host tissues with the prestomal teeth at the end of the proboscis.

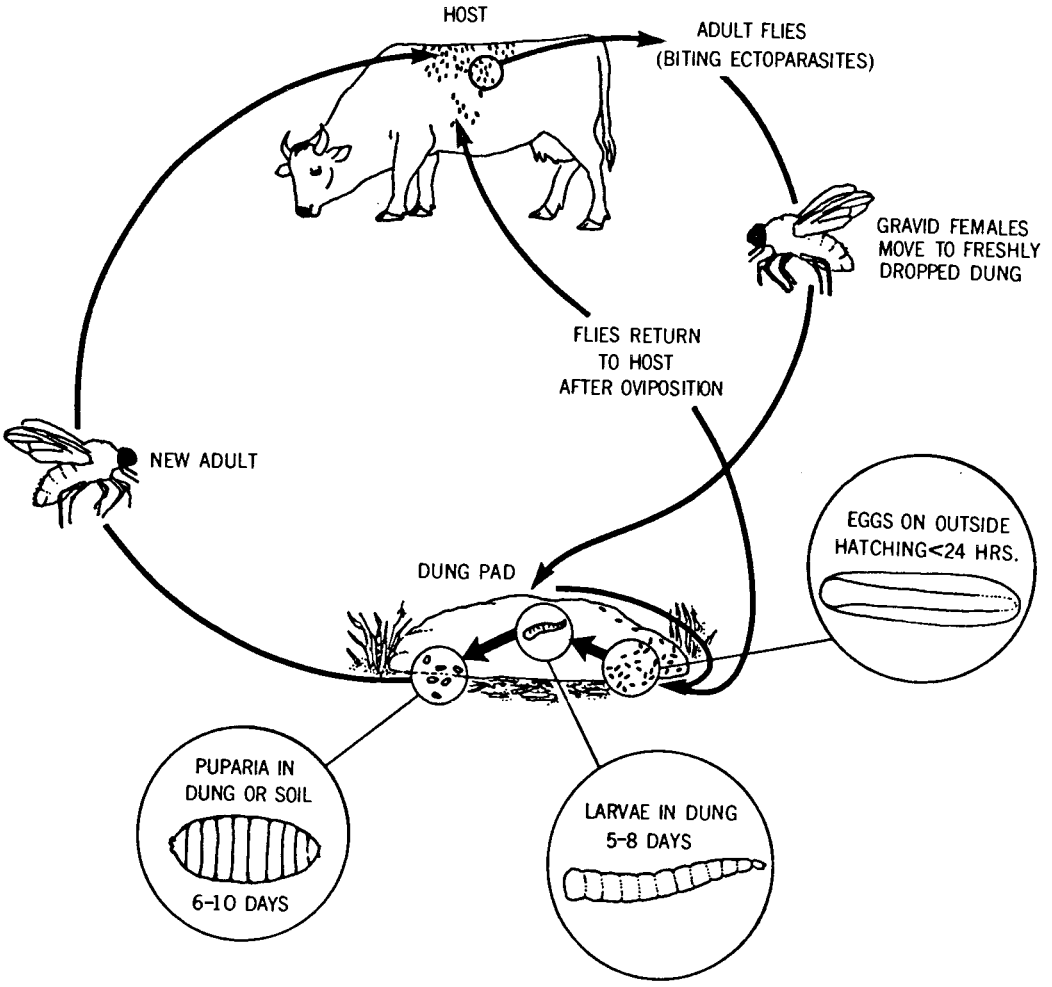
Feeding by horn flies irritates cattle even when only small infestations are present. Bruce (1964) estimated that an infestation of less than 400 flies per animal was not particularly harmful, but noted that 4,000 flies are commonly present on animals in the southern USA, and infestations on individual animals may frequently reach 10,000 flies.

Depner (1961) also recorded up to 10,000 flies on cattle in southern Alberta. Harris and Frazar (1970) calculated that 500 horn flies would remove only about 7 ml of blood from the host per day, and attributed the economic losses caused by horn flies chiefly to irritation. Heavy infestations reduce milk production and weight gain and lessen the thrift and vigor of the animals (Hoelscher and Combs, 1971). Annual economic losses due to horn fly attack are difficult to estimate (Bruce, 1964) but have been placed at $179 million for reduction in weight gain and milk production in the United States (USDA, 1965).

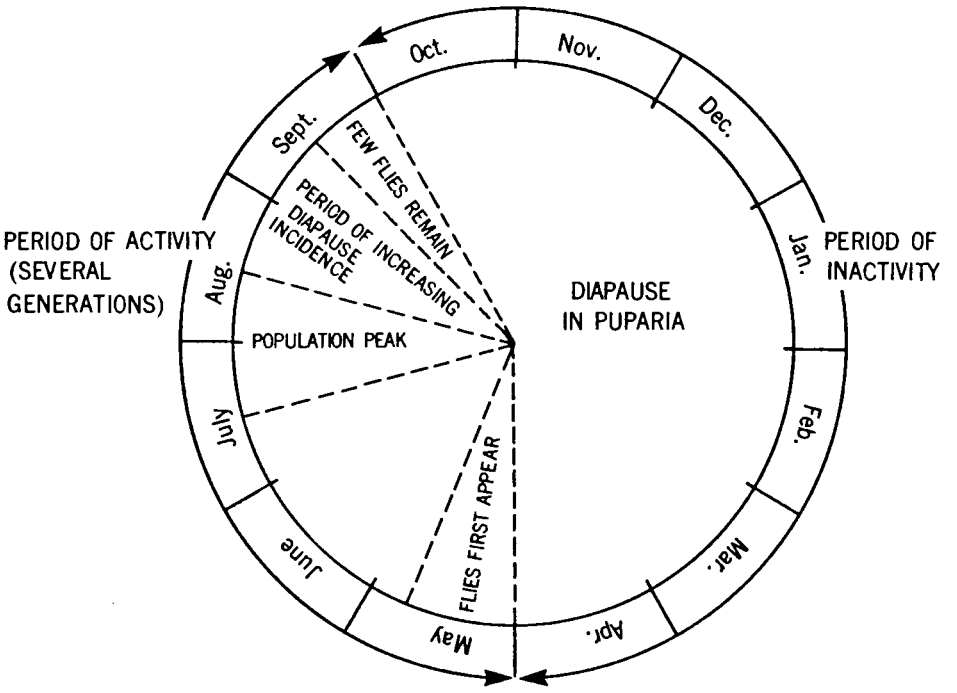
When large numbers of horn flies are present, cattle flick their flanks and backs almost constantly with their tails and spend much time licking themselves, stamping, and rubbing against convenient objects. Repeated rubbing often leads to the formation of sores, which then become a source of attraction for other flies, notably face fly. Horn flies appear to remain on cattle almost continuously, but this was questioned by Hargett and Goulding (1962). Oviposition occurs exclusively on freshly passed feces within the first few minutes after their deposition at any time of the day or night (Bruce, 1964), and the larvae develop within the dung pads. The biology of the horn fly has been described in some detail by McLintock and Depner (1954) and Bruce (1964). Essential features of its life cycle and seasonal history at Kamloops are shown in Fig. 1.

The horn fly was introduced into North America on cattle imported from Europe between 1884 and 1886, and was first reported in Canada from Ontario in 1892 (McLintock and Depner, 1954). It is now found in all Canadian provinces. The flies are present throughout British Columbia (Neilson, 1955) being most important as pests at lower elevations

Figure 1 Life cycle and seasonal history of the horn fly at Kamloops. Times given for the duration of life cycle stages and the seasonal occurrence are only approximate, because they are greatly influenced by climatic conditions.



LIFE CYCLE



SEASONAL HISTORY

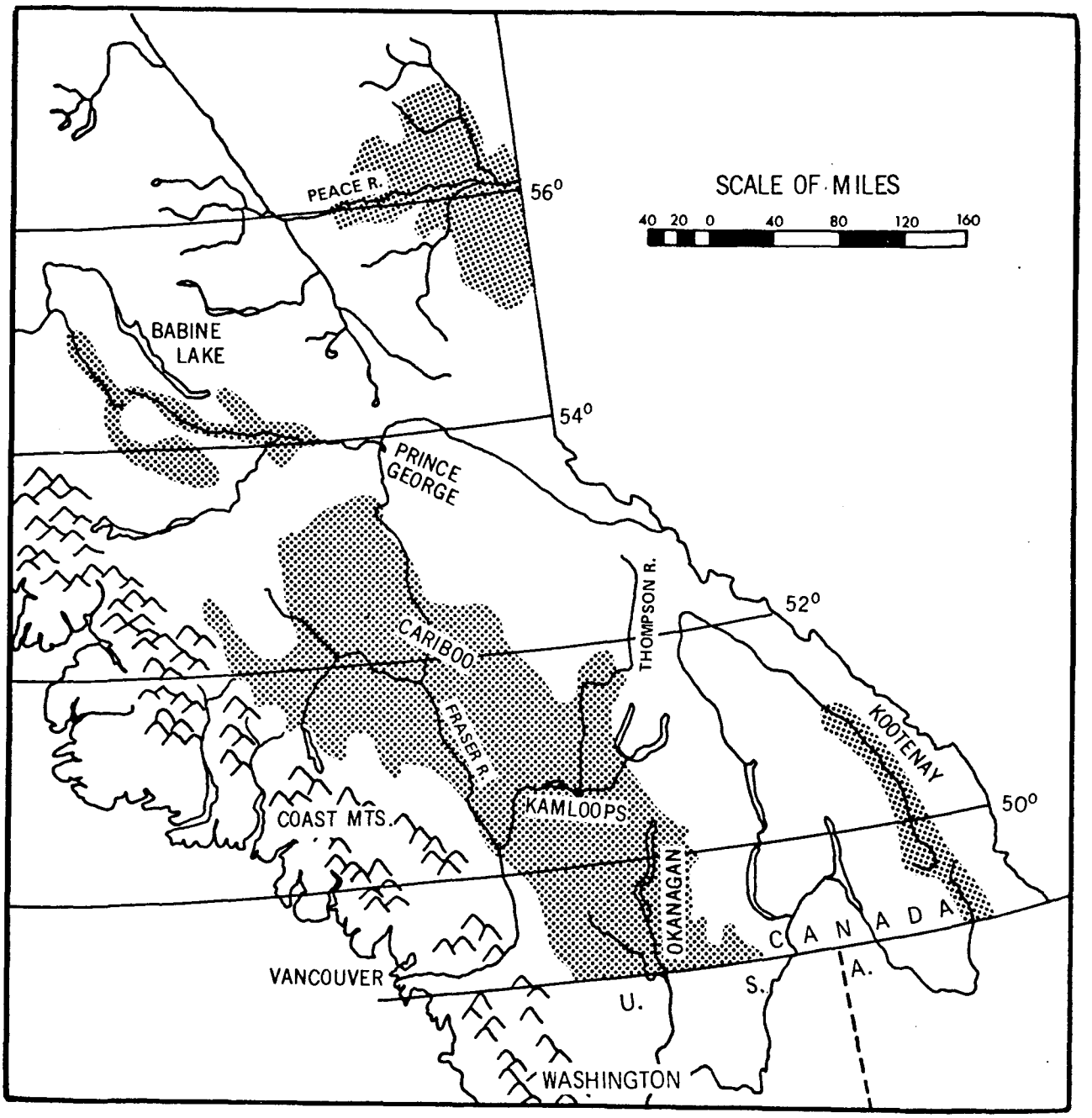
in the Southern Interior, as well as in the adjacent Cariboo and as far north as the Peace River area (e.g., MacNay, 1959) (see Fig. 2). Because the species has a relatively high developmental temperature threshold (Larsen and Thomsen, 1940, cited by Messenger, 1959) its rapid development is favoured in warm environments.

Emphasis in research on the horn fly in North America has until recently centered on aspects of its bionomics, physiology, diapause, and control by chemicals. Poorbaugh (1966) noted that up to that time there had been little consideration of the interrelationships of the horn fly and the face fly with the other members of the dung insect community, and of basic factors determining their distribution and abundance. It is perhaps surprising, considering the amount of research resources that have been directed into chemical control of coprophagous fly larvae as reviewed by Miller (1970), and of their adults, that more attention has not been paid to insect interrelationships in cattle dung pads.

The first comprehensive investigation of a cattle dung insect fauna anywhere in North America was published by Mohr (1943). This work, together with that of Hammer (1941) on coprophagous flies in Denmark and Laurence (1954) on larval inhabitants of cattle dung in England, showed in some detail that dung pads provide a fast-changing environment colonized by a succession of insect species that may differ according to the season and nature of the habitat surrounding the dropping.

Depner (1968) found parasitism to be unimportant in suppressing horn flies over most of their range in Alberta, with the possible exception of northern and western parkland areas. The reports of Lindquist (1936), Bruce (1964), Combs and Hoelscher (1969), and Thomas

Figure 2 Outline showing the major range areas in British Columbia. The Southern Interior for practical purposes may be regarded as bounded by Kamloops in the north, the Okanagan area in the east, and the Coast Mountains in the west (modified from Tisdale, McLean and Clarke, 1954).


SCALE OF MILES
40 20 0 40 80 120 160
PEACE R.
56°
BABINE LAKE
54°
PRINCE GEORGE
THOMPSON R.
52°
CARIBOO
FRASER R.
KOOTENAY
KAMLOOPS
COAST MTS.
50°
OKANAGAN
C A N A D A
VANCOUVER
U. S. A.
WASHINGTON

and Morgan (1972a) indicate that parasites are not important as natural control agents of the horn fly in the United States.

Sanders and Dobson (1966) gathered information on insect interrelationships within cattle droppings in Indiana, including the effect of other insects on horn fly. They found (Sanders and Dobson, 1969) that more horn flies emerged from dung samples that had been exposed in the field for only two hours than from those exposed for up to 12 hours. They attributed this to the reduced competition and predation from other species occurring in pads exposed for the shorter time.

Blume, Kunz, Hogan, and Matter (1970) and Kunz, Hogan, Blume, and Eschle (1972) demonstrated that the presence of other arthropods in cattle droppings markedly reduced the production of horn flies from dung in Texas. Estimates of horn fly mortality caused by the presence of other fauna were in the vicinity of 90%, leaving no doubt that the other arthropods are a potent force in natural regulation of this species, even though their total effect is not sufficient to prevent horn flies from becoming numerous. These authors secured their information by allowing horn fly females to oviposit on field-dropped dung and then excluding all other fauna from some pads while allowing other arthropods access to others. No attempt was made in these investigations to assess either the number of horn fly females ovipositing on the pads, or the number of eggs deposited, and thus to obtain an indication of the actual suppression occurring.

Thomas and Morgan (1972b) found that predators caused up to 95% mortality of horn fly immature stages in Missouri, measured in dung pads that were artificially infested with eggs of the pest.

In British Columbia the horn fly has not been subjected to any

intensive study and the other insect fauna of cattle dung has not been examined. Western Canadian work on this pest has hitherto been performed by scientists of the Canada Department of Agriculture at Lethbridge, Alberta. The investigation described in this chapter examined the diurnal activity, seasonal activity, and the abundance of the horn fly at Kamloops, as well as its potential for progeny production and the effect of other insects in reducing that production.

MATERIALS AND METHODS

The Research Area.

Apart from some preliminary collecting in 1970, all field work was conducted at the Research Station, Canada Department of Agriculture at Kamloops, between May 1 and August 30 in 1971 and 1972.

Kamloops is situated in the bottom of the Thompson River Valley at an elevation of about 1200 feet above sea level (Fig. 2). The land rises rapidly on both sides away from the Thompson Valley to form undulating plateaux lying up to 5000 feet above sea level. This type of topography, where irregular high plateaux are separated from each other by broad deep valleys, is characteristic of much of the grazing land in the Southern Interior of the Province (Tisdale, 1947). The rapid increase in elevation of land above the valley floors causes a marked vertical zonation in climate, soils, and vegetation (Tisdale, 1947).

The climate of the Kamloops area at lower elevations is characterized by warm summers and cold winters that are without continuous snow cover. The frost-free season varies from 160-176 days (Tisdale, 1947).

Some climatic data are given in Table I for Kamloops Airport, which is very close to the Research Station.

Surrounding Kamloops is open grassland range which grades with increasing altitude into open forests of ponderosa pine at elevations generally between 2000-3000 feet. Above this zone occurs Douglas-fir forest, and at the highest elevations the Douglas-fir is replaced by an Engelmann spruce-subalpine fir zone.

The grasslands can be divided conveniently into three zones based on altitude, available moisture, soil, and plant associations (Tisdale, 1947). These are known as the lower, middle, and upper grassland zones. The higher areas of grassland and forested zones receive more precipitation than the lower grassland, and at the same time moisture effectiveness increases with altitude due to reduced evaporation (Tisdale, 1947). Grassland is the most productive range, but makes up only about a sixth of the total range area (Mason and Miltimore, 1969). It limits the carrying capacity of the whole range area because it is used for spring, fall and winter grazing, while the forested range, though much more extensive in area, can only be used for summer grazing (Tisdale, McLean, and Clarke, 1954).

Cattle overwinter at the lower elevations. They are released from their wintering paddocks in mid-April, and as spring progresses they are herded up into the higher regions of the grassland, and finally into the forested zones where they spend the whole summer. Some dairy and beef cattle are maintained on irrigated pastures in the valley floors, where there are some feedlots for beef cattle also.

Cattle left in the valleys suffer the most irritation from horn fly, which along with other fly pests is usually controlled with

Table I Mean monthly temperatures and precipitation for Kamloops Airport, B.C. (50°43'N; 120°25'W).+

Month	Mean maximum temperature (°C)			Mean minimum temperature (°C)			Mean precipitation (mm)		
	Normal	1971*	1972*	Normal	1971*	1972*	Normal	1971*	1972*
January	-2.3			-9.7			28.6		
February	3.1			-5.8			15.4		
March	9.1			-2.1			8.1		
April	14.3			0.8			12.4		
May	21.8	22.2	22.9	6.8	7.2	7.5	19.0	23.0	14.2
June	25.2	22.3	23.3	10.8	10.4	11.5	36.2	35.9	34.4
July	29.1	29.9	28.2	12.7	12.7	12.4	25.8	15.4	18.2
August	27.6	31.2	29.2	11.8	14.4	13.1	26.8	12.4	19.2
September	22.4			7.6			20.2		
October	13.8			3.0			18.5		
November	5.4			-2.0			20.2		
December	1.1			-5.8			28.1		
							259.3		

+ From the records of the Kamloops Weather Office, Atmospheric Environment Service, Canada Department of the Environment.

* Normal values (adjusted to the period 1941-1970) are compared with actual figures only for the months during which field investigations were conducted.

insecticides. Range cattle may not be attacked so heavily, possibly due to their continued movement over a large area throughout the summer and also because of the cooler temperatures at the higher altitudes which slow down fly development. Moreover, the horn fly favours an open sunny habitat (Hammer, 1941) so that cattle which spend a lot of time feeding in heavily timbered range may not be bothered by them to any extent.

There are difficulties inherent in investigating the dung insect fauna associated with cattle feeding on open range. To follow the life processes of the horn fly it was necessary to utilize individual dung pads from the moment of deposition onwards, and this can be done only with extreme difficulty in open rangeland.

Because of this, a herd of cattle on irrigated pasture at the Research Station was used as a source of basic information on production and activity of horn flies and other insects. In 1971, 29 fully grown Hereford heifers and one bull were used in the investigation, and in 1972 this number was reduced to 14 of the original animals, plus calves. The cattle grazed pastures consisting of a mixture of bromegrass, orchardgrass, and Ladino clover. They were removed to fresh pasture every two or three weeks. After each change of pasture, no insect sampling was performed for at least a week to allow dung insects to move into the new pasture from surrounding areas, and to avoid the worst of the scouring which occurs in cattle when they eat fresh rich forage.

Sampling Procedures.

a) Horn fly production.

A single sampling technique was used to measure the production of horn flies from dung pads in both the presence and the absence of other insects. Because the horn fly is active day and night, the sampling work had to quantify fly production during all hours of the day (i.e., a time span of 24 hours). This was thus taken as the standard length of sampling period (hereafter known as "sampling period"). However, 24 continuous hours of sampling work were never undertaken. Instead, each 24-hour sampling period was completed in a series of sessions: initially, four 6-hour sessions, and later in the season, two 12-hour sessions. These were always completed with a pause of 24 hours between the end of one session and the beginning of the next. For example, using 12-hour sampling sessions, a sampling period which began with a session from 0600-1800 would end with another 12-hour session beginning on the next day at 1800 and ending at 0600 on the day following that. Each sampling period was arbitrarily divided into eight 3-hour time intervals for recording insect activity, e.g., 0000-0300, 0300-0600, and so on. Thus a sampling session of 12 hours contained four 3-hour time intervals.

Six sampling periods were completed between 9 June and 23 August, 1971. Two more were completed in June and July in 1972, but these, for reasons explained later, were only of 18 hours' duration.

Gravid female horn flies arrive at a fresh dung pad just after a cow has finished defecating, though a few may land on the dung even before the completion of the act. The flies mill about briefly on the surface of the dung, and then most move beneath the pad within 30 seconds.

Some return to the top surface before moving again to the underside of the pad, while others fly directly from the underside and search for a host. When the weather is warm, all flies leave within five minutes of their arrival. Some eggs are deposited on the upper surface of the pad, but most are placed underneath, either on the dung or on plant material close to it (Bruce, 1964). It is obviously impracticable to count the eggs that have been laid. Fortunately, the synchronous ovipositional behavior of the adults enabled them to be trapped as they left the dropping. The number of adults captured at each dropping could then be used as an index of potential progeny production.

The sampling procedure (Fig. 3) consisted of following the cattle about the pasture and observing defecation. Sixty seconds (timed by a stopwatch) after a suitable pad was dropped, it was covered with a net. This interval of 60 seconds allowed female horn flies in the vicinity to arrive, but they were then prevented from escaping after they had oviposited.

The net (Fig. 4) was lined on the inside with fine white nylon mesh which rose within the frame to join an inverted funnel fixed into the metal lid of a clear 20 oz polystyrene container (trap). The net was covered with heavy black cotton cloth on the outside, so that when viewed from within, only the exit at the top showed daylight. As horn flies are strongly phototactic they quickly moved upwards through the funnel and into the trap.

Ten minutes after the pad had been deposited, the net was removed, after shaking to encourage any remaining horn flies to move up into the trap. Pads were then either covered to exclude other insects (covered pads) or left exposed to allow natural colonization by other arthropods

Figure 3 Sequence of operations employed in the horn fly sampling work.

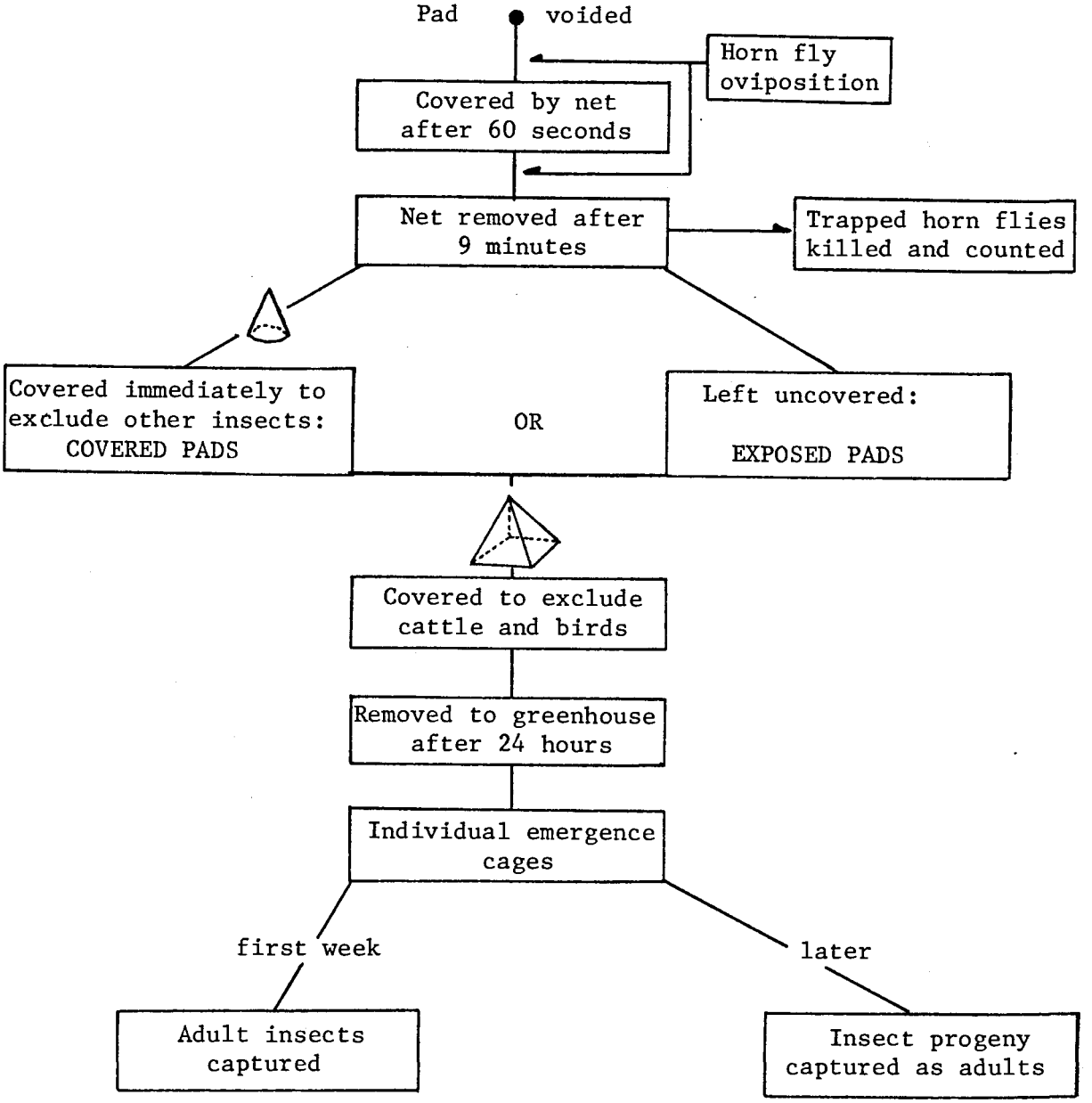
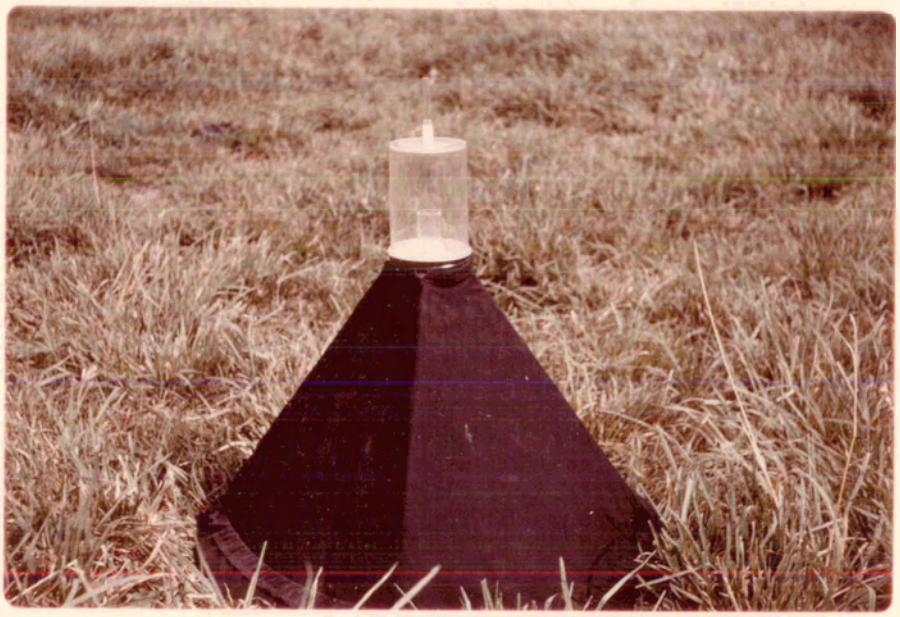
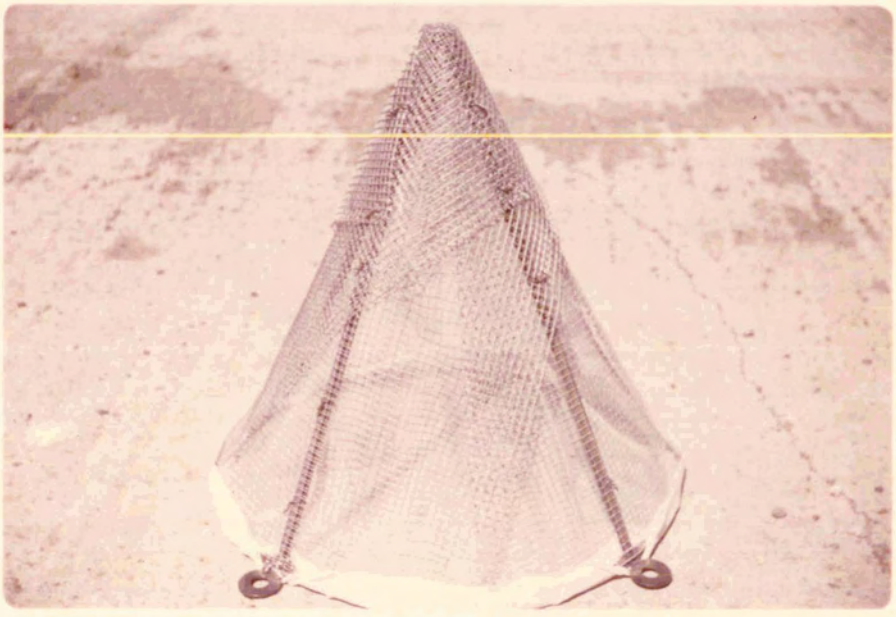

Pad
voided
Horn fly oviposition
Covered by net after 60 seconds
Net removed after 9 minutes
Trapped horn flies killed and counted
Covered immediately to exclude other insects: COVERED PADS
OR
Left uncovered: EXPOSED PADS
Covered to exclude cattle and birds
Removed to greenhouse after 24 hours
Individual emergence cages
first week
later
Adult insects captured
Insect progeny captured as adults

Figure 4 Net and trap used for collection of ovipositing horn flies.

Figure 5 Wire mesh cage with inner nylon mesh cone used to exclude other insects from covered pads.





(exposed pads). Covered pads had a stout conical 40-cm diameter metal and mesh cage placed over them, which was spiked to the ground. A fine nylon mesh cone was fitted to the interior of the wire mesh cage (Fig. 5). The junction of the cage with the ground was covered with a little soft earth that was tamped to reduce the chances of insects interfering with the covered samples. All pads were then enclosed by a larger heavy metal wide-mesh cage (base was 120 cm square; Fig. 6). The processing of each sample took 15-20 minutes.

At the time each dropping was being processed a record was made of the identification number of the animal (all were equipped with numbered neck chains), the time, pad consistency, wind speed, and amount of cloud. These factors were noted to assist in an understanding of horn fly bionomics and for a possible guide in accounting for any aberrant results in the sampling. Pad consistency was visually estimated and given one of the following gradings: very thin, thin, average, thick, very thick (after Sanders and Dobson, 1969). Pads classified under the two extremes were never used in case they are inimical to horn fly development, as suggested by these authors. Most pads taken were of average consistency. Wind speed was roughly estimated by the method outlined in Peterson (1964). Temperature and relative humidity were recorded on a thermohygrograph protected by a weather box placed on pasture just outside the paddock being grazed. The sensors in the thermohygrograph were about six inches above the ground.

Horn flies trapped at each dung pad were anaesthetized with carbon dioxide and transferred to individual killing bottles for subsequent examination and counting.

Pads were removed from the field after 24 hours. A sharpened spade was used to cut 1-3 cm vertically into the soil just outside the perimeter of the dropping. This allowed a small divot to be lifted with

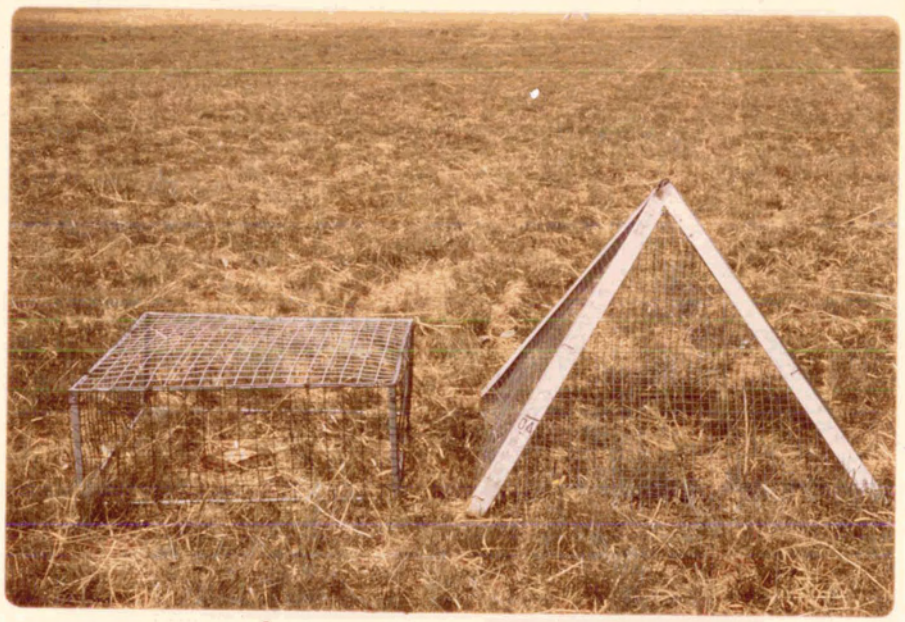
Figure 6 Two types of large-mesh frame used during the dung insect investigations to prevent interference from cattle and birds. The frame on the right was used for all sampling work that measured horn fly production. The frame on the left was used in some other field experiments.

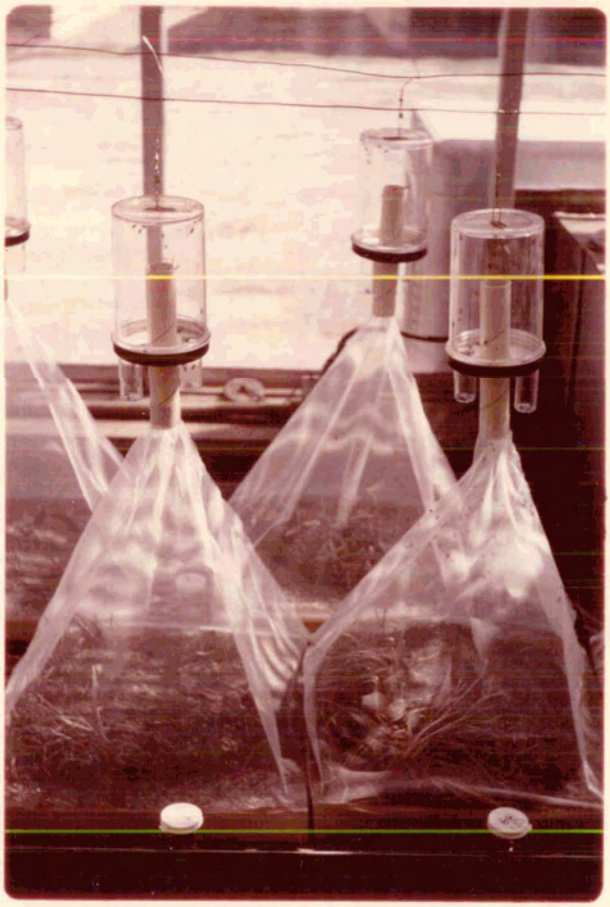
Figure 7 Greenhouse emergence cages.

the pad. Most of the insects situated beneath the pad were thus retained. Each pad on its soil base was placed on a cardboard tray in a larger square carrying tin whose lid had large, mesh-covered holes for aeration. Tins were transported several miles to a greenhouse and the pads were transferred to individual mesh cages, which used the same principle for trapping emergent fauna as those described by Poorbaugh (1966), although they were constructed of different materials. In this work, heavy 30 x 30 x 3 cm cardboard trays were used instead of Poorbaugh's metal tins, and the nylon mesh was affixed to the cardboard with masking tape (Fig. 7). A shallow layer of vermiculite was spread on the bottom of the cardboard tray before a pad was introduced. At the top of the cage, the nylon mesh was attached to a rough cardboard tube projecting through the centre of the lid of an inverted 20 oz polystyrene jar. Insects appeared to have no trouble making their way up through the cardboard tube into the trap, and here the adult insects originally contained in each pad assembled and were removed for identification and counting. The larvae derived from these and from other adults (e.g., the various flies which had visited the pad while it was in the field) were able to complete their development and find their way up into the trap. Insects which had been unable to reach the trap and therefore died in the enclosure with the dung pad were collected and their numbers were added to the totals of those trapped.

A hand-drawn cart with large wheels were specially constructed for the sampling work. On it was carried all the equipment required for the sampling operation (Fig. 8), and between samplings it was used when collecting dung pads from the field.

Figure 8 Hand-drawn cart used in the field sampling work.





Ideally, equal numbers of pads were covered or exposed during each 3-hour time interval, up to a maximum of three of each treatment per interval. This made a theoretical maximum number of 48 pads attainable during a sampling period of 24 hours. A number of factors such as poor dung quality, unavailability of pads, and darkness, were responsible for preventing this number of pads from ever being taken in any single period.

Night sampling was difficult. A spotlight and flashlight were used when locating and processing each pad. It is essential to be able to hear droppings fall at night to find them, and the continuous noise produced by an oil refinery close to the Research Station undoubtedly caused the loss of some acceptable pads.

A total of 186 pads were processed in 1971, of which 177 were usable, and 61 were taken in 1972. The raw data on horn fly production from each pad consisted of the number of females that originally were trapped after oviposition, and the number of adult progeny derived from them. To facilitate comparisons of progeny production between pads, the number of ovipositing females was divided into the number of progeny produced to give the mean number of adult progeny produced by each female trapped (hereafter known as progeny per female).

The number of progeny per female in the case of both covered and exposed pads fitted a Poisson distribution. Consequently, prior to statistical analysis, a square root transformation ($\sqrt{x+1/2}$) was applied to the data (Sokal and Rohlf, 1969). The data for number of females trapped at pads approximated a normal distribution (skewed to the right) and were transformed logarithmically before statistical analysis (Sokal and Rohlf, 1969).

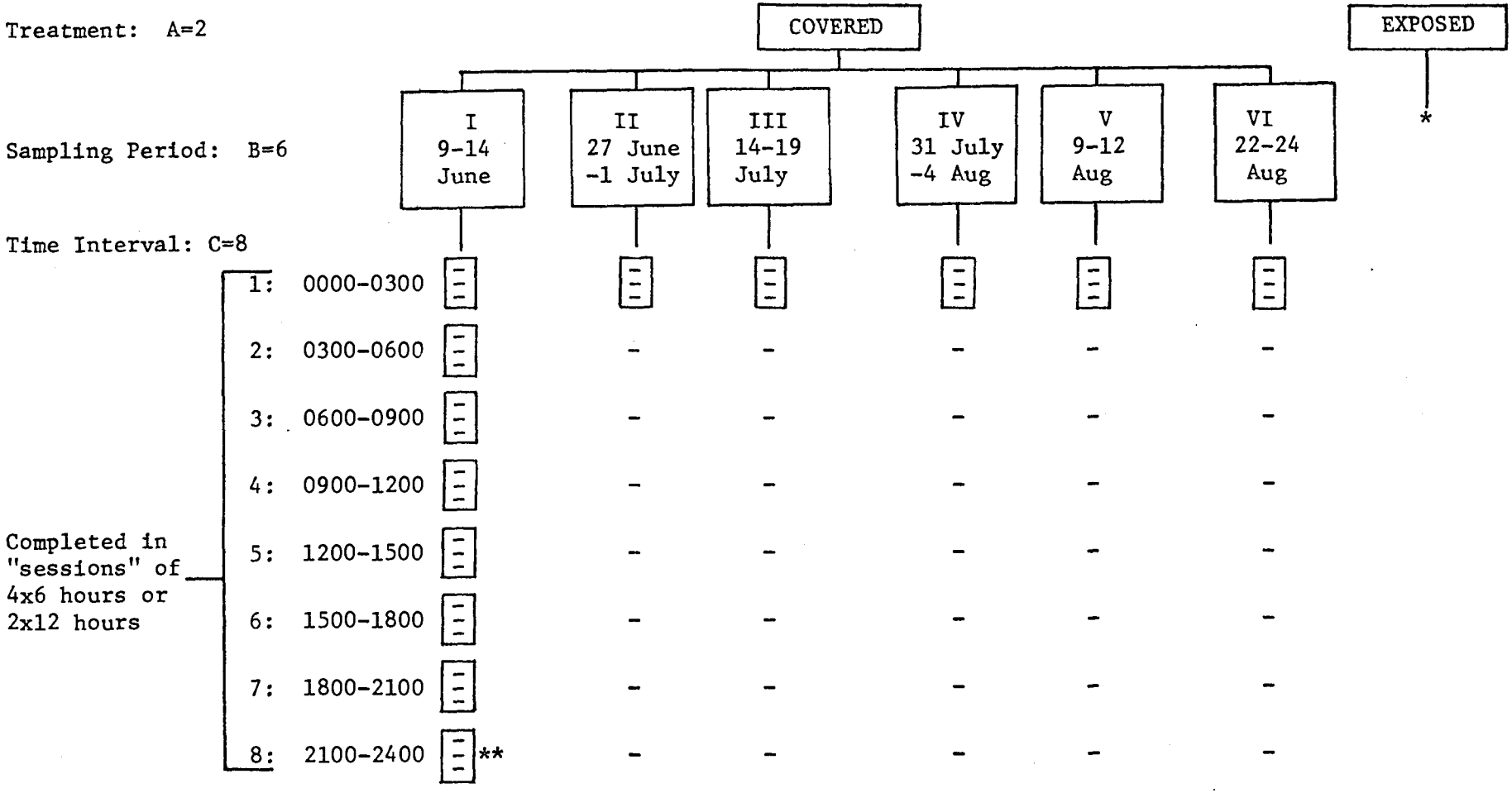
An analysis of variance (anova) was then performed on the horn fly data (progeny per female) to determine whether significant differences existed between treatments (covered and exposed pads), sampling periods and time intervals using the computer program (SFU AVAR 23) for unequal sample sizes.

The sampling schedule and anova model are outlined in Fig. 9. As the between-treatment anova showed high levels of significance for treatment, sampling period and time interval, other separate anovas were employed to examine the differences in progeny produced per female within each treatment, and to test for significant differences between and within sampling periods and time intervals. A similar model was employed for data on the number of ovipositing females, except that allowance was made for a maximum of six replicates instead of three (i.e., in this case values were contributed by all pads sampled, irrespective of their subsequent treatment).

b) Diurnal activity patterns of insects other than horn fly.

The sampling technique described in (a) yielded the absolute number of adult insects that exposed pads contained after they were left in the field for 24 hours. Diurnal activity patterns of the insects could not be determined by this method. To gather information on these, trap sampling of insects other than horn fly was conducted on June 19 and July 19, 1972. Sticky traps were made from 10 x 10-cm squares of thin plywood which were liberally smeared with "Stikem Special" adhesive (Michel and Pelton Co., California). These were sunk into the tops of 1,000-g artificial dung pads, so that the top surface of the dung was level with the Stikem surface. A nail driven through the centre of each

Figure 9 Horn fly sampling schedule for 1971. This also formed the anova model for comparison of the progeny produced per female between and within treatments. The basic model was again used when examining data on the number of female flies trapped at pads.



* Levels B and C and the replicates repeated as for the covered pads.

** Three replicates: in many time intervals it was impossible to obtain this number of pads.

square facilitated its placement and removal (Fig. 10).

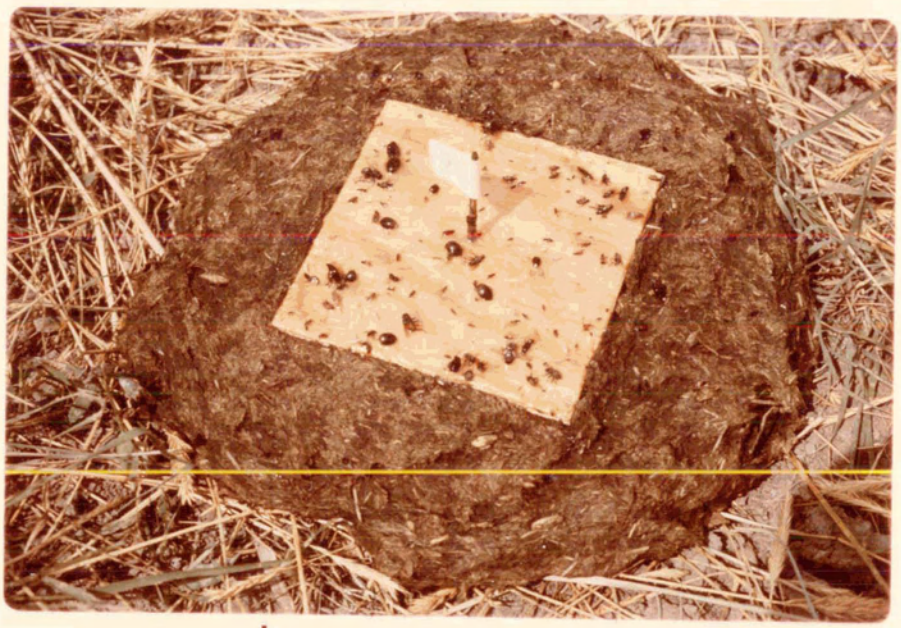
Insects walking over the dung surface often came in contact with the Stikem; others land directly on it, and many of these became mired in it after the initial contact. This provided a simple method of assessing the relative abundance of most insects attracted to fresh dung at various times of the day.

Except for the horn fly activity, dung insect movement is markedly reduced at night. The activity sampling was therefore conducted only in daylight and near-daylight hours. Two fresh pads bearing sticky traps were set out about 50 yards apart in the pasture at 0300 hours and covered with large open mesh frames to prevent interference from cattle or birds (Fig. 6). The traps were removed every three hours and their pads covered with soil to eliminate any attraction for insects. Another pair of fresh dung pads and traps was then put out. The last pair of sticky traps was collected at 2100 hours. Insects were identified and counted in situ in the laboratory.

c) Colonization of dung by insects other than horn fly.

One experiment in 1971 was to determine if 24 hours in the field were sufficient to allow adequate colonization of exposed pads by other species of insects, especially those that are potentially harmful to the horn fly. Mohr (1943) stated that the major colonization of fresh dung pads by insects (i.e., species that utilize dung of this particular age) occurred during this time. This finding was indirectly supported by that of Blume et al. (1970) who found no significant difference between the numbers of horn flies produced by pads exposed to other insects (some inimical to horn fly) for either 6 or 24 hours. The results of Finne and Desiere (1971) and Kessler and Balsbaugh (1972)

Figure 10 Sticky trap used for assessment of insect activity patterns.



show that some coprophilous Coleoptera reach their peak populations within 24 hours after the pad is voided.

Six artificial dung pads weighing 1500 g were placed in a cattle pasture in July 1971, arranged in line and 25 paces apart. The cattle-proof large mesh frames covered each pad. Three pads were removed after 24 hours by selecting alternate pads along the line. These were placed in Berlese funnels and their insects were extracted into alcohol. The remaining three pads were removed after 48 hours' exposure in the field and their fauna was extracted in the same way.

d) Parasitism of horn fly.

Parasitic Hymenoptera were not commonly seen in the greenhouse emergence cages that housed pads taken during the horn fly sampling work. The pads were removed from the field after 24 hours, and quite possibly this did not allow time for colonization by all potential parasites. Some of the very small species may have been able to pass through the 0.8-mm mesh on the emergence cages. Moreover, the method of breeding out the fauna in pads made it impossible to relate emerged parasites to their true hosts.

In 1972 attempts were made to estimate the degree of parasitism on horn fly. A bait trapping method was used. On two occasions four aluminum foil dishes containing 1000-g artificial dung pads which contained 300 horn fly eggs near hatching (5 July) or 300 young larvae (14 July) were placed out in the pasture, and protected by large mesh frames from cattle and birds. The eggs were counted onto small squares of filter paper (Depner, 1961), placed on the centre of the top of the pads, and were protected by small inverted funnels of filter paper with their edges dipping into the dung. The filter paper squares were

retrieved later for recording of percentage hatch. When larvae were used they were counted onto the dung surface. The pads were collected after seven days in the field.

e) Predators of the horn fly.

The sampling work in (a) that investigated horn fly production also provided information as to its likely insect predators. The two most prominent of these were then used in field and greenhouse experiments in an endeavour to define their individual and combined effects on horn fly production.

Both species are beetles, of which one is predaceous in either the adult or larval stage whereas the other is predaceous only as a larva. They were collected from dung pads taken in the open rangeland within two or three days of deposition. The pads were held in greenhouse emergence cages and predators emerged into the traps. Beetles were separated according to species and held at 20°C in pint cartons containing damp facial tissues until required. Collection of pads containing predators was made about 36 hours before the start of the experiment.

Early in the day of the field experiments, the predators were anaesthetized with moist carbon dioxide, sorted, and assigned to the various replicates. The effect of the short period of anaesthesia on the beetles was examined and no harmful consequences were noted. Equal numbers of males and females were used where possible. Predators were placed in ventilated plastic petri dishes filled with damp facial tissue and having short cork legs affixed to the underside.

Experiments started at 0900 hours. When a suitable pad was deposited the female horn flies were netted from it in exactly the same fashion as in the earlier sampling work. A dish containing predators was

then placed on the dung before it was covered with the standard conical insect excluding frame (Fig. 5). Predators were then liberated into the enclosed space by lifting the lid of their petri dish from the outside by means of a length of fusewire.

Some of the pads selected, in a regular sequence, were covered in the normal way but left untreated to estimate potential horn fly production. These constituted controls.

The single greenhouse experiment employed three-quart milk cartons cut down to make pots that were filled to 4 cm depth with moist soil, which was covered with a standard quantity of chopped dry grass stalks. This simulated field conditions where dung is usually dropped on grass and is supported by this above the soil surface to some extent; predators were thus afforded easier access to the underside of the pads where they had additional cover. Fresh dung was collected and formed into 250-g pads in the containers, and 100 horn fly eggs were placed on all of these. Predators were confined within the pots with gauze covers.

RESULTS

Insects Associated with Fresh Cattle Dung at Kamloops.

A large number of dung insect species emerged from the samples collected in the field. A few species in addition to these were taken occasionally during other field work. Appendix I lists these insects. The list is not exhaustive because this investigation was mainly concerned with certain types of insects which breed in the dung, namely:

- prevalent coprophagous species that might be important basic units in food chains within the pads, and which, along with the horn fly, are probably exclusive inhabitants of fresh dung;

- predaceous and parasitic insects that utilize the coprophagous species;
- species that manipulate the dung mass.

Coffey (1966) and Poorbaugh, Anderson, and Burger (1968) gave extensive lists of flies associated with cattle dung in southeastern Washington and in California, respectively. These authors collected flies that were attracted to dung, as well as those reared from it, and it is likely that some of the species they mention are present at Kamloops but are not listed in Appendix I because they do not breed in cattle dung. Some species that actually breed in dung may have been omitted because of their erratic occurrence or low numbers but it is highly unlikely that any moderately prevalent dung-breeding species are not included. Nearly all the species present at higher elevations in the grassland and timber zones were taken at dung in the irrigated pasture, though sometimes there were differences in the relative numbers of a species colonizing dung in the two situations.

Where possible the geographical origin of each species was determined, either from the literature or by communication with the authority responsible for the identification. Species are designated exotic if there is documentation that they were introduced into North America since the arrival of the Europeans and native if it is considered that they have a natural Nearctic distribution. For many species that currently have a Holarctic distribution, it is impossible to determine an area of origin with certainty. These have a question mark (?) in the column designating their origin (Appendix I). If for these Holarctic species there is some but not definitive evidence for a certain origin, the question mark appears after the possible origin, e.g., Native?

An assessment by family of the origins of the insects listed in Appendix I follows:

ORDER	NUMBER OF IDENTIFIED SPECIES	
	Known or thought to be native	Known or thought to be exotic
COLEOPTERA	13	15
DIPTERA	9	10
HYMENOPTERA	5	-

Horn Fly Production in the Absence of Other Insects

The diurnal and seasonal oviposition pattern of the horn fly was assessed from the counts of adult females that were trapped as they left the fresh dung during 1971. Additional information was obtained during the two supplementary sampling periods carried out in 1972. It was assumed that all females trapped at pads had been ovipositing.

Potential horn fly production in the field was estimated by horn fly progeny that emerged from the covered pads. Usually few, if any other insects managed to gain access to these. Occasionally Philonthus cruentatus and Sphaeridium scarabaeoides beetles were taken from covered pads, having usually reached them while they were being processed.

The number of horn fly females trapped at each covered pad together with that of their progeny was used to measure the number of offspring per female that grew to maturity in any time interval. Regression of the number of adult progeny produced per pad on the number of parent females trapped showed a highly significant relationship ($P<0.001$) for six out of the eight 3-hour time intervals (the other two were significant at

$P<0.01$ and $P<0.05$), and for all eight intervals combined ($N=86$; $Y=2.11 + 5.15X$; $r=0.825$). Use of the latter relationship as an index of the number of eggs laid would assume that there was no difference in natural mortality of immature stages arising from eggs laid in each time interval. It is not known at this time if natural mortality (used here to mean all causes of mortality other than by arthropods) varies with time of oviposition.

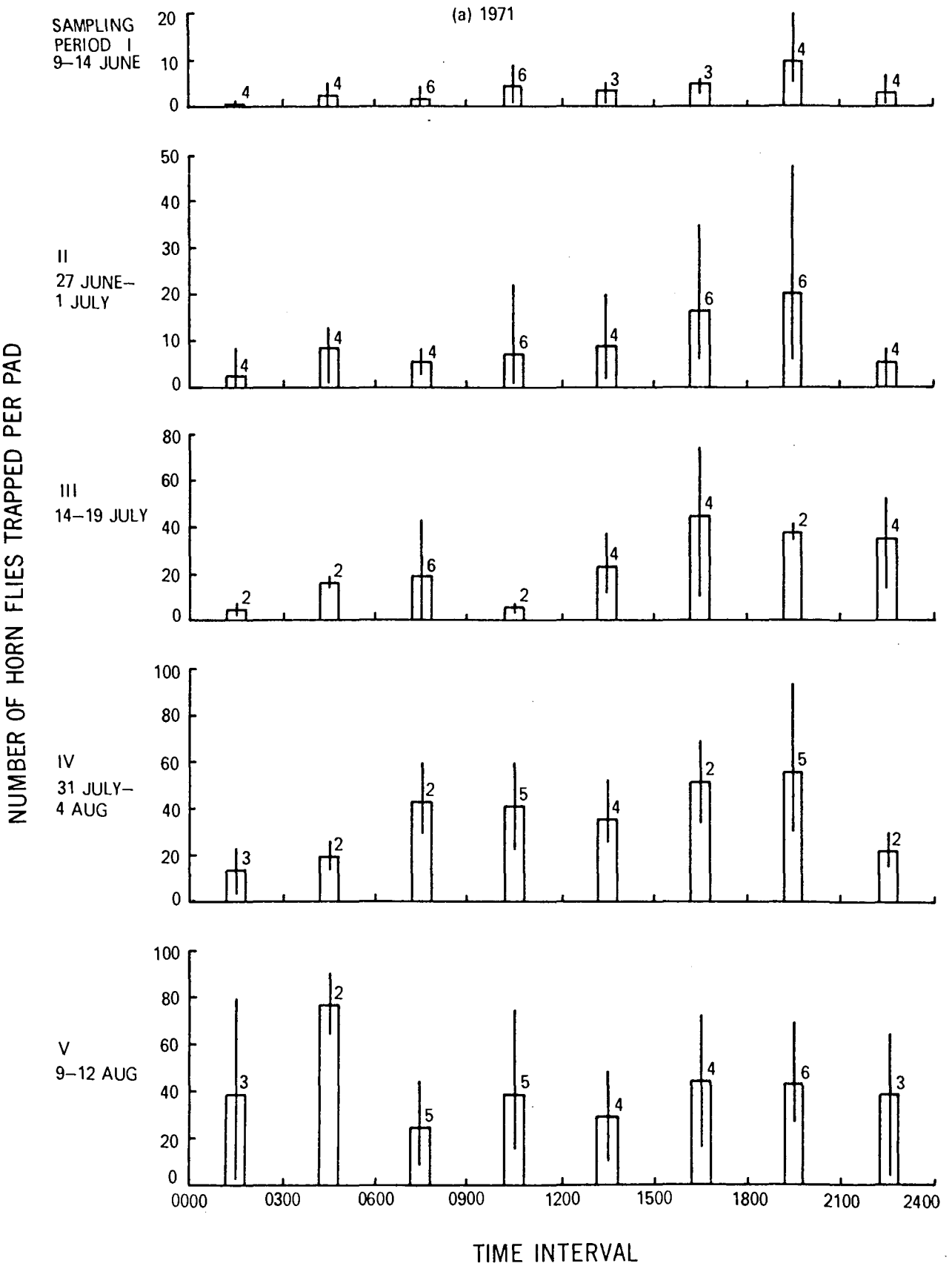
a) Diurnal and seasonal oviposition pattern of females.

The diurnal oviposition pattern of horn fly females is represented in Fig. 11 for the sampling periods in 1971 and 1972. There is no constant pattern evident in the number of female flies that visited fresh pads throughout the day. In some sampling periods (e.g., II, III, IV in 1971 and especially I in 1972) there is a trend of gradually increasing numbers of ovipositing females from early morning until the 1800-2100 interval, after which (i.e., in darkness) there was an apparent decline. In the others this trend was not evident. Occasionally some male horn flies were trapped along with the females, but in no case did the number ever exceed three per pad.

Anovas of the female horn fly data showed highly significant differences between sampling periods and between time intervals in the number of flies trapped at pads; there were also significant differences in the number of flies trapped within most sampling periods and time intervals (Appendix II, Table 1). Data therefore could not be pooled for the season in either case.

Seasonal variation in the numbers of female horn flies trapped at fresh dung pads in 1971 is shown in Fig. 12. Large ranges in the numbers trapped were encountered in all sampling periods. Results

Figure 11 Diurnal variation in the number of female horn flies trapped at fresh dung pads during 1971 and 1972. For each time interval the range and mean are presented. The number of observations is given beside each mean.


(a) 1971
SAMPLING PERIOD I 9–14 JUNE
II 27 JUNE–1 JULY
III 14–19 JULY
IV 31 JULY–4 AUG
V 9–12 AUG
NUMBER OF HORN FLIES TRAPPED PER PAD
TIME INTERVAL
0000
0300
0600
0900
1200
1500
1800
2100
2400

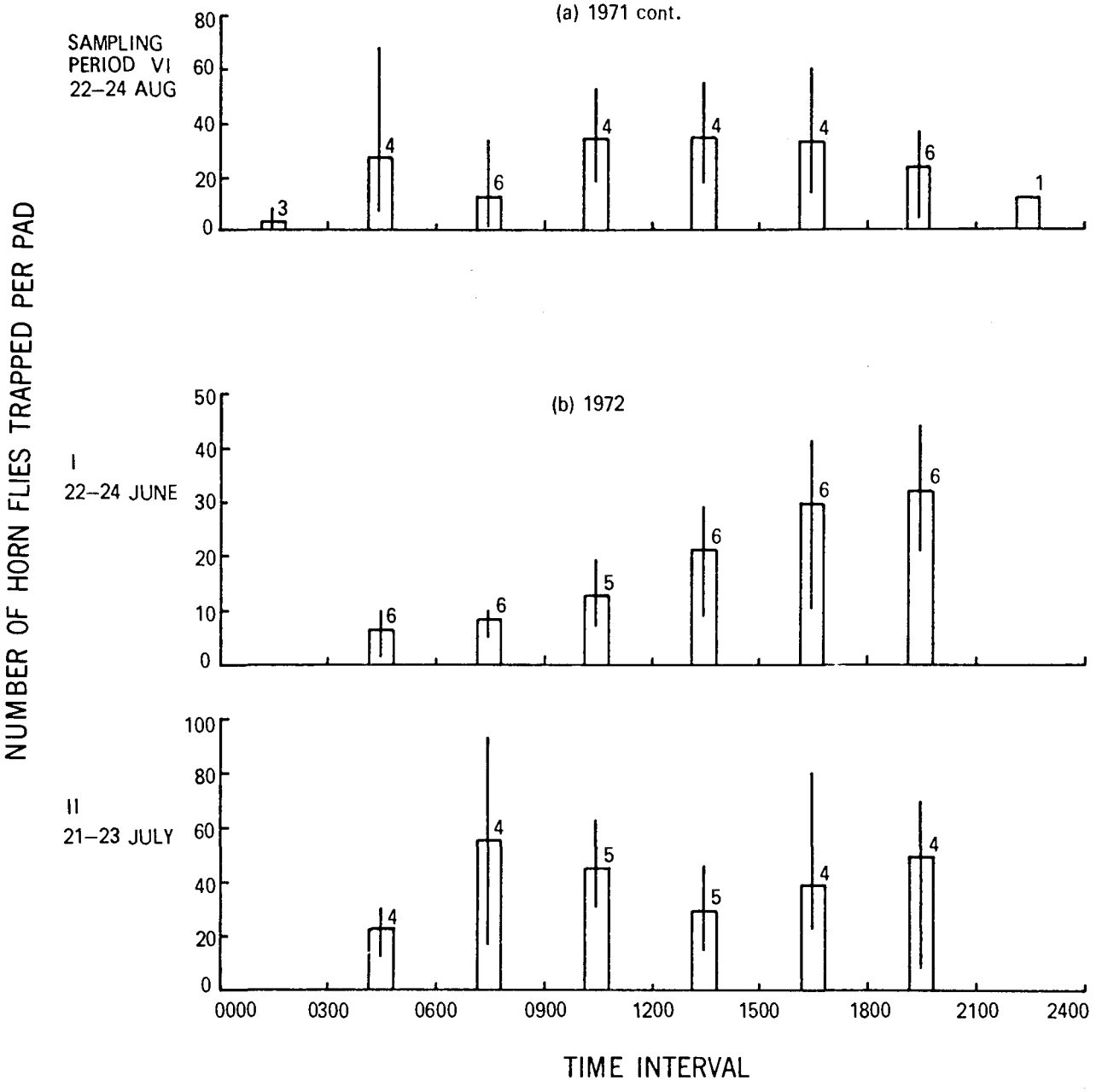
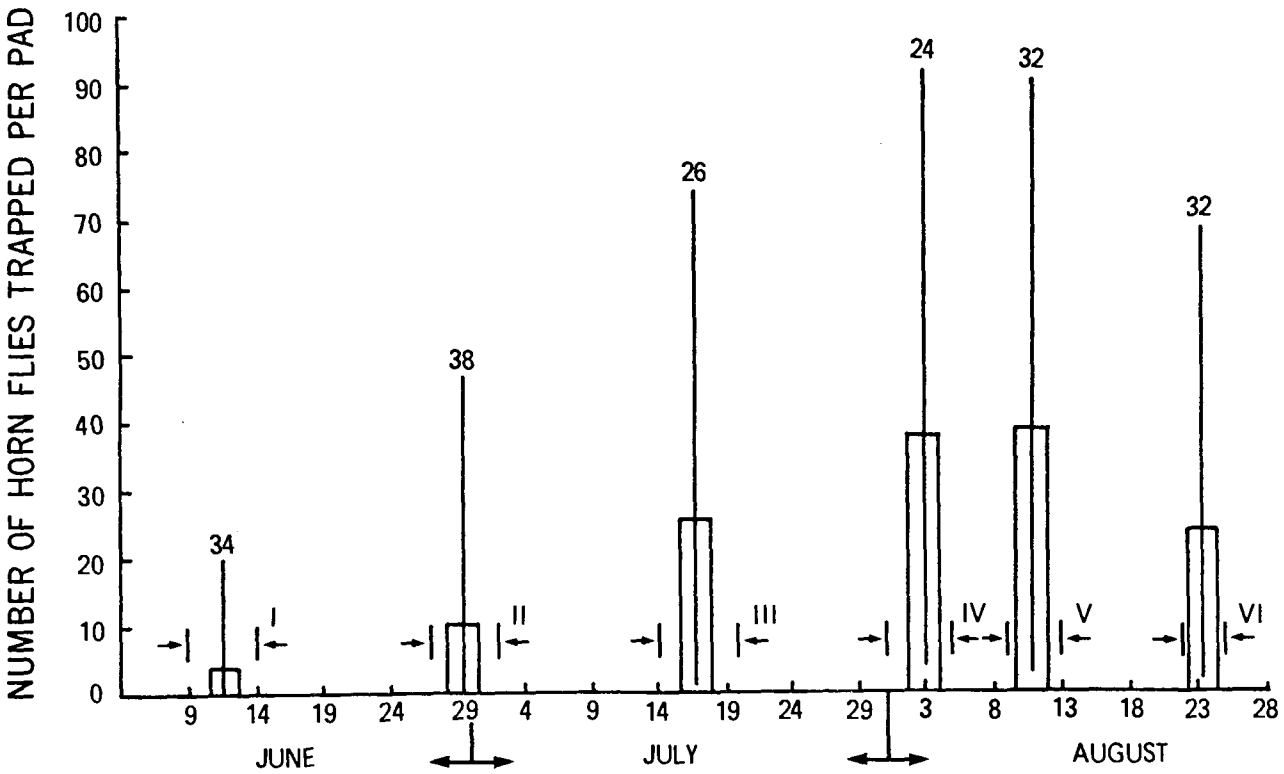

(a) 1971 cont.
SAMPLING PERIOD VI 22–24 AUG
80
60
40
20
0
3
4
6
4
4
4
6
1
(b) 1972
I 22–24 JUNE
50
40
30
20
10
0
6
6
5
6
6
6
II 21–23 JULY
100
80
60
40
20
0
4
4
5
5
4
4
0000
0300
0600
0900
1200
1500
1800
2100
2400
TIME INTERVAL
NUMBER OF HORN FLIES TRAPPED PER PAD

Figure 12 Seasonal variation in the number of female horn flies trapped at fresh dung pads during 1971. For each sampling period the range and mean are presented with the number of observations above each range. The duration of each sampling period is indicated by short arrows and vertical lines above the abscissa.


NUMBER OF HORN FLIES TRAPPED PER PAD
100
90
80
70
60
50
40
30
20
10
0
34
38
26
24
32
32
I
II
III
IV
V
VI
9
14
19
24
29
4
9
14
19
24
29
3
8
13
18
23
28
JUNE
JULY
AUGUST

show a trend of increasing average number of flies trapped as the season progressed. Peak numbers of flies were trapped in late July and early August, presumably corresponding to a peak in horn fly numbers on cattle during this period. From that time onwards, replacement of flies suffering natural mortality decreased due to an increasing proportion of the population becoming immobilized as diapausing pupae.

Some horn flies oviposited whenever fresh dung was passed, except when numbers on cattle were very low (e.g., early in the season) or when low temperatures inhibited their activity.

Horn fly activity is dependent on ambient temperatures (Bruce, 1964). As soon as sunshine reached the pasture and air temperature rose in the early mornings, a noticeable increase in fly activity occurred. The flies were sluggish at dung on cool mornings. Allowance was made for this when netting the adults which at such times did not ascend quickly into the trap. The net therefore was kept in place for another five minutes (total netting time was then 14 minutes). After this time any flies not in the trap were on the net or the dung surface and were easily counted, and their number was added to that of the trapped flies. Very high temperatures also appeared to reduce the number of flies attracted to pads.

When temperatures were warm, the first horn flies generally appeared in the trap within 30 seconds of placing the net over a pad. The fact that generally several minutes were required for all netted horn flies to enter the trap was evidence that oviposition was not unduly disturbed by the black net; otherwise, it would be expected that most of the flies would have entered the trap simultaneously as soon as the net was placed over the dropping. Most or all of the flies often were in the

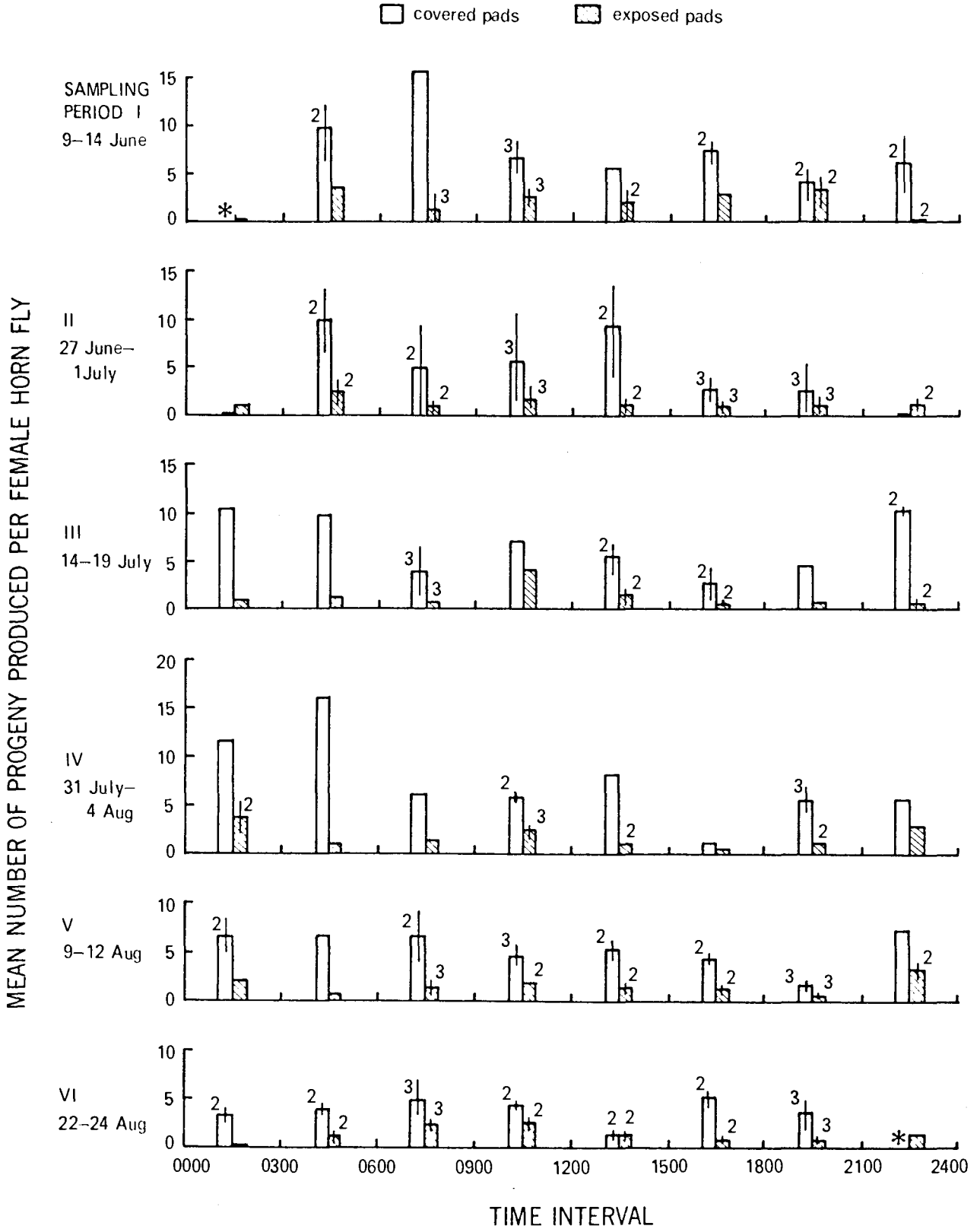
trap within five minutes after the deposition of the pad. Tests made by substituting a second net for the original after the first ten minutes showed that on all but the coldest mornings all flies were in the trap within 10 minutes.

Because of their coordinated response to defecation of the host, the majority of horn flies that oviposit on a pad probably come from its producer, especially when this animal is some distance away from other cattle. When other cattle are in close proximity to a defecating beast, some of their own horn flies are probably attracted to the fresh pad. Marked differences were noted in size of horn fly infestations on individual cattle and these generally persisted throughout the season. No correlation was detected between the horn fly infestation of an animal and the number of horn flies attracted to its pads. Because of the great variability encountered in numbers of flies ovipositing on covered pads in any sampling period, and the low number of pads observed for individual animals (range 0-8 for a total of 86 pads from 30 cattle) the possibility that there is a correlation between the two variables should not be discounted.

b) Diurnal and seasonal progeny production.

The number of progeny produced per female horn fly when other insects did not have access to pads (covered pads) is shown in Fig. 13, representing all sampling periods in 1971. As observations are completely missing for covered pads in the 0000-0300 interval in I, and also for the 2100-2400 interval in VI, the method of Yates (Steel and Torrie, 1960) was used to estimate one value for each interval, after which the anovas were completed and adjustments made to total and error degrees of freedom where necessary.

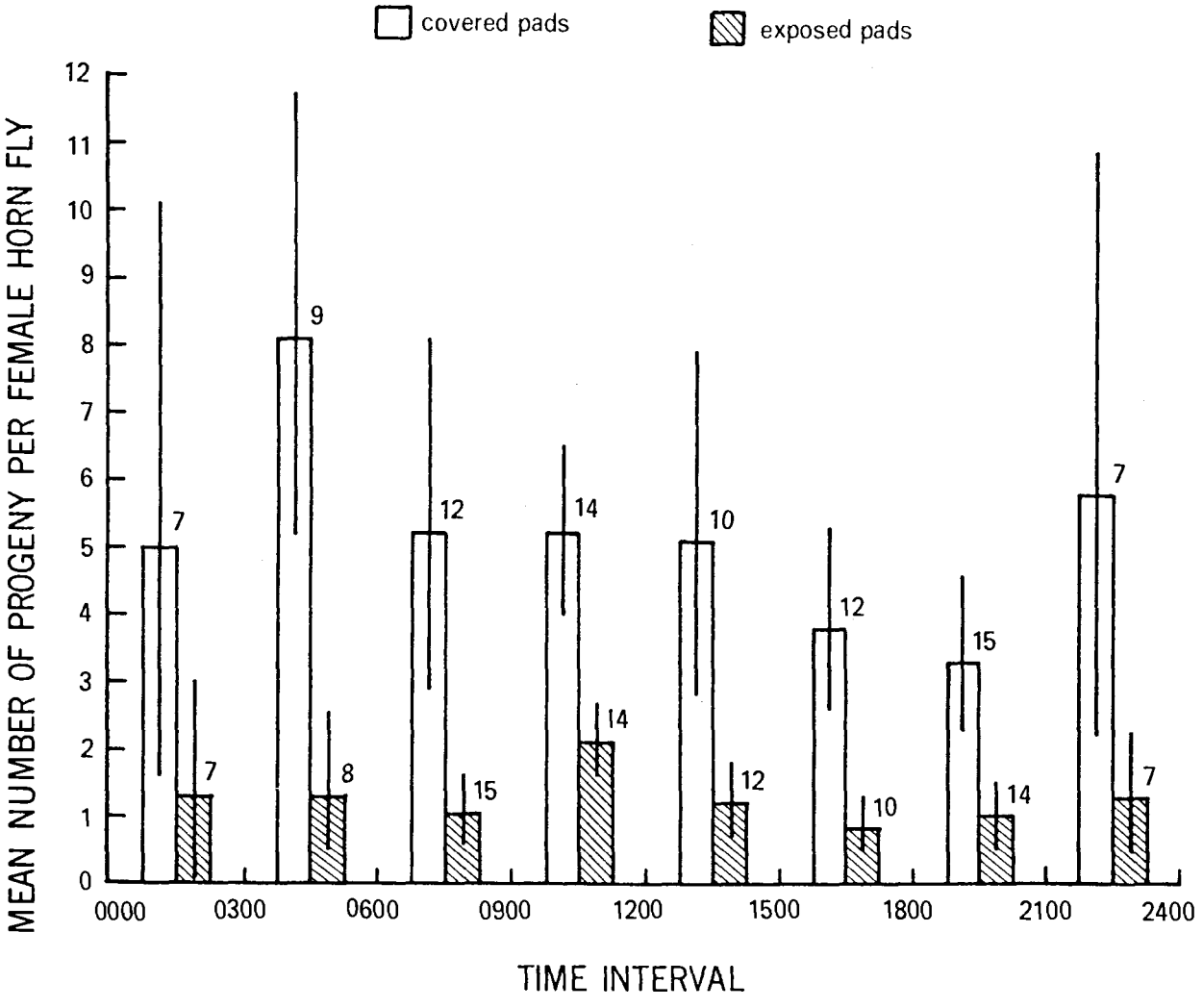
Figure 13 Number of horn fly progeny that emerged from covered and exposed pads during 1971. The range of estimates of the mean number of progeny produced per female horn fly and the overall mean are presented for each time interval. The number of observations is indicated by a figure close to each mean. Absence of a figure beside a mean indicates a single observation. An asterisk indicates that no observation was made.


covered pads
exposed pads
SAMPLING PERIOD I 9–14 June
II 27 June–1July
III 14–19 July
IV 31 July–4 Aug
V 9–12 Aug
VI 22–24 Aug
MEAN NUMBER OF PROGENY PRODUCED PER FEMALE HORN FLY
TIME INTERVAL
0000
0300
0600
0900
1200
1500
1800
2100
2400

Anovas of the data for progeny production of covered pads showed significant differences between sampling periods and time intervals, and within sampling periods, but not within time intervals (Appendix II, Table 3, covered pads). The data for each time interval could therefore be pooled for the six sampling periods, and are presented in Fig. 14 (covered pads). There was a trend toward greatest progeny production per female in the early morning, and least in the early evening. Significant differences between means in time intervals (as indicated by the anova above) were located by use of the t-test. It was found that in the 0300-0600 time interval, significantly more progeny per female were produced than in the following intervals: 0900-1200, 1500-1800, and 1800-2100. Also, progeny production in the 1800-2100 interval was significantly lower than in the 0900-1200 and 2100-2400 intervals (and the 0300-0600 interval already mentioned).

The trend of greater progeny production per female fly in the early morning was confirmed in two more sampling periods in 1972. Sampling was conducted from 0300-2100 (i.e., 18 hours only) because this period included both the 0300-0600 and 1800-2100 intervals, that had shown the greatest apparent difference in number of progeny per female throughout 1971. Progeny per female in the 0300-0600 interval was significantly higher than that in any other interval for both sampling periods (Appendix II, Table 4). In all other intervals progeny production was remarkably uniform. In the 0300-0600 interval of the first sampling period in 1972, 20 progeny were produced per female. This is approximately twice the number produced in the corresponding interval in the second sampling period, 1972, and 2.4 times the mean value obtained for this

Figure 14 Number of horn fly progeny that emerged from covered and exposed pads during each time interval in 1971. Data were pooled for the six sampling periods and the values presented are means and their confidence intervals (retransformed to original scale of measurement), with number of observations near each mean.


covered pads
exposed pads
MEAN NUMBER OF PROGENY PER FEMALE HORN FLY
TIME INTERVAL
0
1
2
3
4
5
6
7
8
9
10
11
12
0000
0300
0600
0900
1200
1500
1800
2100
2400
7
7
9
8
12
15
14
14
10
12
12
10
15
14
7
7

time interval in 1971 (Fig. 14).

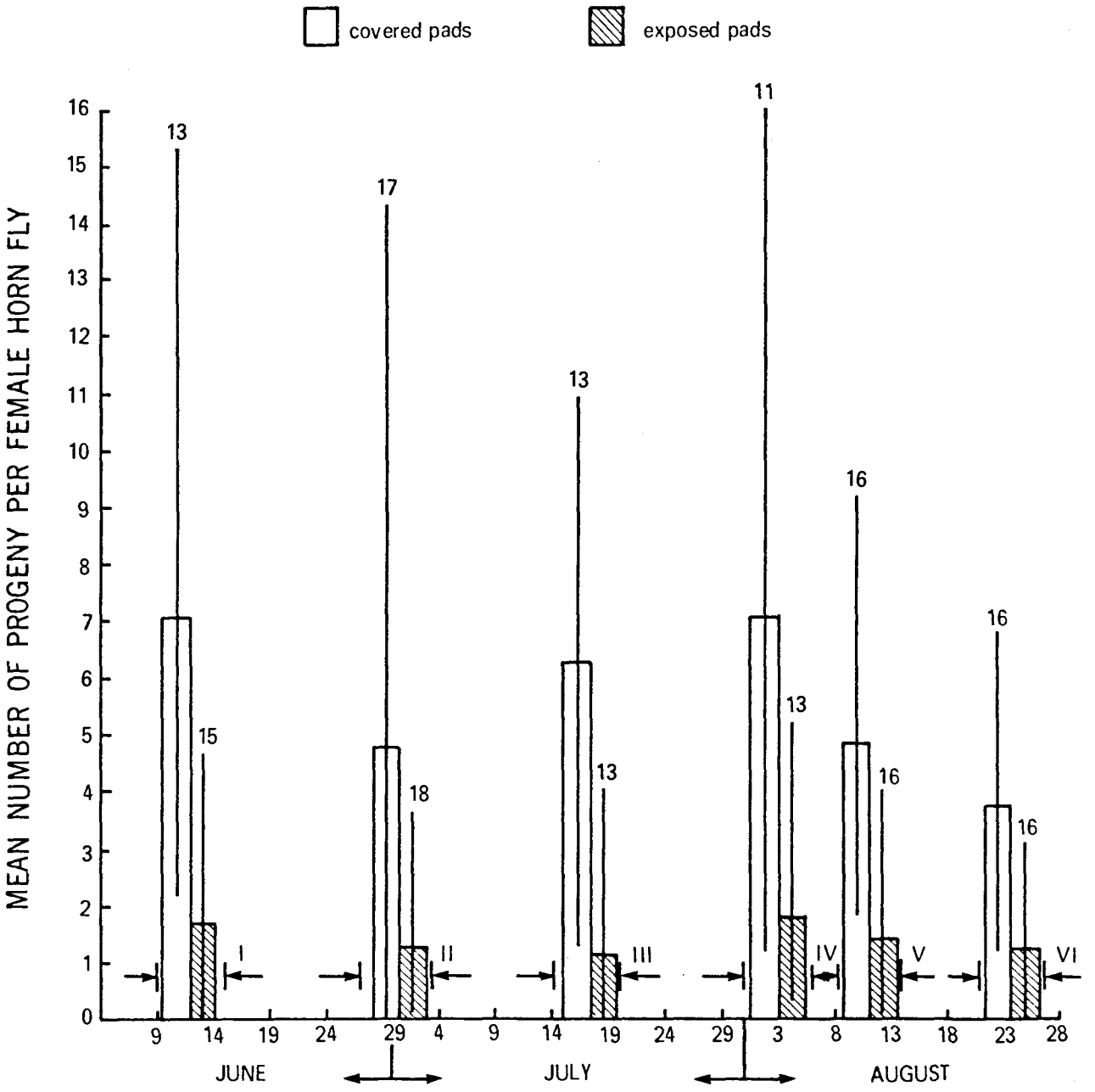
There are several possible explanations for the observed differences in number of progeny per female developing from eggs laid at various times of the day. One of the most likely is that there is in fact a diurnal rhythm in oviposition, with greatest numbers of eggs being laid by females during the 0300-0600 interval.

The progeny produced per female for each sampling period when other insects did not have access to pads is shown in Fig. 15 (covered pads). Significant differences within one sampling period (Appendix II, Table 3) prevented pooling of the data for each. Progeny production ranged between similar wide limits for sampling periods I, II, and IV. After this there occurred a narrowing trend in the range of V and VI as the horn fly activity season was drawing to a close. Many diapausing pupae were encountered in the final sampling period (VI). The pads taken during this period were placed in a cold room at 1.6°C for four months to break diapause, then held at 27°C and 70% relative humidity until insects ceased to emerge. The implications of this will be considered later when reviewing the effect of other insects on horn fly production.

The greatest number of progeny reared from a single large covered pad was 658 flies derived from 79 ovipositing females in mid-August, 1971. Yields of over 400 flies per pad were uncommon.

It is not known how many eggs are normally laid by a female horn fly per oviposition, but it is probable that they never deposit their full complement on one pad. Bruce (1964) recorded the normal full complement of eggs in nulliparous flies as 24. On two occasions in this investigation, the remaining eggs were dissected from 20 horn flies caught during the sampling (i.e., after at least one oviposition

Figure 15 Number of horn fly progeny that emerged from covered and exposed pads during each sampling period in 1971. The ranges of progeny produced per female fly are given together with overall means. Numbers of observations appear at the top of each range.


covered pads
exposed pads
MEAN NUMBER OF PROGENY PER FEMALE HORN FLY
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
13
15
17
18
13
13
11
13
16
16
16
I
II
III
IV
V
VI
9
14
19
24
29
4
9
14
19
24
29
3
8
13
18
23
28
JUNE
JULY
AUGUST

opportunity). The number of eggs remaining ranged from 0 to 32.

Horn Fly Production in the Presence of Other Insects.

a) The gross effect of other insects on horn fly production.

Colonization of fresh dung commenced the moment a new pad was dropped. Horn flies arrived first and shortly thereafter many species of flies and beetles found the pad and remained for varying periods of time. Female horn flies often laid one or more eggs on the top surface of the pad before moving to the underside. As many as six eggs were laid in this location by individual females. Other prevalent coprophagous muscoid flies (e.g., Ravinia spp., and Orthellia caesarion) larviposited or oviposited on the dung in the few hours before a firm crust formed, as did many other dipterous species. The beetles remained in or beneath the dung, their numbers rising and falling at a much slower rate than was evident for the flies. With certain of these species there may be frequent interchange of individuals between fresh pads. However, in each pad there is for each beetle species a net gain in numbers followed by a net decline as the pad ages.

Table II shows the number of beetles that were present in artificial dung pads after being exposed when fresh to natural colonization in the field for two different time periods. Many of these beetles are predators of the horn fly, or in competition with it. In all but one case there were more individuals present after 48 hours' exposure than after 24; however, most of the potentially important species were well represented after 24 hours, especially Sphaeridium. The effect on horn fly of the groups or species listed in Table II is discussed later in this chapter.

Table II Number of individuals of various beetle species that were present in artificial dung pads exposed when fresh for two different times to natural colonization by insects in irrigated pasture at Kamloops, July, 1971. Three replicates of each exposure time were used.

Species or group	Number of Beetles			
	Exposed 24 hours		Exposed 48 hours	
	Mean	Range	Mean	Range
Sphaeridium scarabaeoides	66	29-96	68	61-81
Sphaeridium lunatum	24	13-42	39	15-58
Sphaeridium bipustulatum	5	1-11	2	2-5
Philonthus cruentatus	14	12-16	46	41-56
Total Staphylinidae	17	14-22	53	47-63
Onthophagus nuchicornis	59	36-80	100	40-132
Aphodius fossor	-	-	2	0-4
Aphodius fimetarius	15	10-20	74	10-118
Small Aphodiinae	27	6-58	69	38-126

1) Diurnal variation in the effect of other insects: The effect of other insects on horn fly production was measured by comparing the mean number of progeny produced per female for the covered pads (i.e., without other insects) with that produced by exposed pads (i.e., with other insects) in each time interval. Figure 13 shows the effect of the presence of other insects on horn fly production for each of the six sampling periods in 1971. Covered pads tended to produce more progeny per female than exposed pads. Horn flies usually emerged 1-2 days earlier from exposed pads than from covered pads taken at the same time. In the following evening time intervals the number of adult progeny produced per female fly for the covered pads was zero, and therefore less than or equal to the number of progeny produced by the exposed pads: (i) 0000-0300, sampling period I; (ii) 0000-0300 and 2100-2400, sampling period II; and (iii) 2100-2400, sampling period VI.

These anomalous results were caused either by total lack of ovipositing females, by females which for some reason produced no progeny, or by total absence of covered pads during one time interval.

Substantial suppression of horn flies occurred due to the presence of other insects. There was a highly significant difference in the number of progeny produced per female between covered and exposed pads (Appendix II, Table 2). There were also significant differences in progeny per female for treatment between sampling periods and between time intervals.

As previously described, separate anovas were then employed for covered and exposed pads, comparing progeny per female between and within sampling periods and time intervals (Appendix II, Table 3). No

significant differences in progeny per female were detected within time intervals for covered pads; however, there were differences within 2 out of the 8 time intervals for exposed pads. These differences were present in the 1500-1800 and 2100-2400 time intervals (Appendix II, Table 3(c)). Further examination of the data in these two intervals showed that the significant differences were due to two single values and one pair of values that were unusually higher or lower than the others in the interval. As the records showed good biological reasons for suspecting that these were aberrant results, to accept the significant differences present in the two intervals would thereby cause a type I error (Sokal and Rohlf, 1969). The aberrant results were discarded and the remaining data pooled for exposed pads in each time interval for 1971 (Fig. 14).

Differences between the means for exposed pads in Fig. 14 were tested by the t-test. More progeny per female were produced by exposed pads in the 0900-1200 interval than in the 0600-0900, 1200-1500, 1500-1800, and 1800-2100 intervals, but not in the 0000-0300, 0300-0600 or 2100-2400 intervals. There were however no gross fluctuations in the number of progeny produced per female by exposed pads throughout the day.

The significance of differences between pairs of means in each time interval (Fig. 14) was found by use of the t-test (Appendix II, Table 5). In all intervals, the mean number of progeny per female produced by exposed pads was significantly lower than the corresponding number for covered pads. Per cent suppression of horn fly varied from 60 in the 0900-1200 interval to 83 in both the 0300-0600 and 1500-1800 intervals [% suppression = 100 (covered progeny - exposed progeny) / covered progeny]. Suppression of horn fly caused by the presence of other insects thus was substantial at all times of the day.

A comparison of suppression values does not reveal the complete details of insect-caused mortality. Figure 14 shows that there were big differences in the actual reduction of progeny per female at various times of the day when other insects were present. Values ranged from 2.3 progeny per female in the 1800-2100 interval to 6.8 progeny per female in the 0300-0600 interval. It remained to be determined as to which species were responsible for the greatest reduction in horn fly numbers.

2) Seasonal variation in the effect of other insects: Significant differences were found within sampling periods for progeny per female from covered and exposed pads (Appendix II, Table 3(b)). While only one sampling period was involved in each case, examination of the original data showed no reason to suspect that any values should be rejected. Therefore the data could not be pooled for the season in the same fashion as was done for time intervals.

Seasonal variation in the mean number of progeny produced per female horn fly in 1971 is shown in Fig. 15. The covered pads have been dealt with already. Inspection of Fig. 15 suggests that a relatively constant and lower number of progeny per female emerged from exposed pads throughout the season, so that suppression of horn fly by other insects was always substantial.

There is a trend of decreasing number of progeny per female evident for covered pads in the last two sampling periods (V and VI). A similar trend is not apparent for exposed pads in V and VI. It has been mentioned that many diapausing pupae were encountered in the pads taken during VI and that these pads were kept over the winter and subjected to cold treatment to break diapause. Emergence of diapausing individuals was

thus obtained artificially early in the 1972 spring. This treatment may have caused extra horn fly mortality in VI as compared to the other five periods; it would have decreased the number of progeny produced per fly. Any severe mortality in VI caused by cold treatment would, however, have occurred in both the covered and exposed pads instead of in the covered pads only. Because there was no apparent decline in the number of progeny per female produced by exposed pads, this may be evidence that the cold treatment did not affect survival in VI significantly. Alternatively, if the effect of other insects on horn fly was reduced in late August, it would cause a relative increase in the number of progeny per female produced by exposed pads. This would counteract to some extent any decrease in progeny production of exposed pads that was caused by the cold treatment. Counts of other insects from exposed pads taken in VI showed slightly more Staphylinidae but only one third as many Sphaeridium beetles in comparison with V. These two groups are thought to be major predators on horn fly; the reduction in numbers of Sphaeridium may have eased predation pressure in VI.

Diapausing horn flies may have been present in V, but were not recorded. It is unlikely that there were many. Some of the larvae would have been predisposed to enter diapause at that time, but they probably would not have done so because of very high ambient temperatures (Depner, 1961) that prevailed then (up to 38°C maximum). Sampling period VI was completed under much cooler conditions.

b) The individual effects of other insects on horn fly production.

1) Parasitism: Recovery of puparia during the two field trapping experiments in 1972 was always very low (maximum 22 puparia/300 larvae). This caused suspicion that the method used for establishing eggs or larvae was inviting added attention from predators. Per cent parasitism of puparia recovered ranged from 0 to 19. Parasites recovered were Spalangia haematobiae and Muscidifurax raptor. It thus appears that parasitism of the horn fly is relatively unimportant at Kamloops in comparison with other insect-related mortality factors.

2) Predation: The insects that were collected with exposed pads taken during each sampling period emerged in two distinct groups:

i) the adults (mainly Coleoptera) that were within or beneath the pad when it was removed from the field after 24 hours, and which emerged in the ensuing 7-10 days;

ii) adults of Coleoptera, Diptera, and Hymenoptera which developed in the pad as the progeny of (i).

The horn fly suppression was caused by the combined action of both the adults in (i) and the larvae in (ii), because each group contains known natural enemies of fly larvae.

Prevalent insects in (i) were:

Scarabaeidae: Onthophagus nuchicornis; several species of small Aphodiinae; and a few of the much larger Aphodius fimetarius and A. fossor.

Hydrophilidae: Sphaeridium scarabaeoides; S. lunatum; S. bipustulatum; and Cercyon spp.

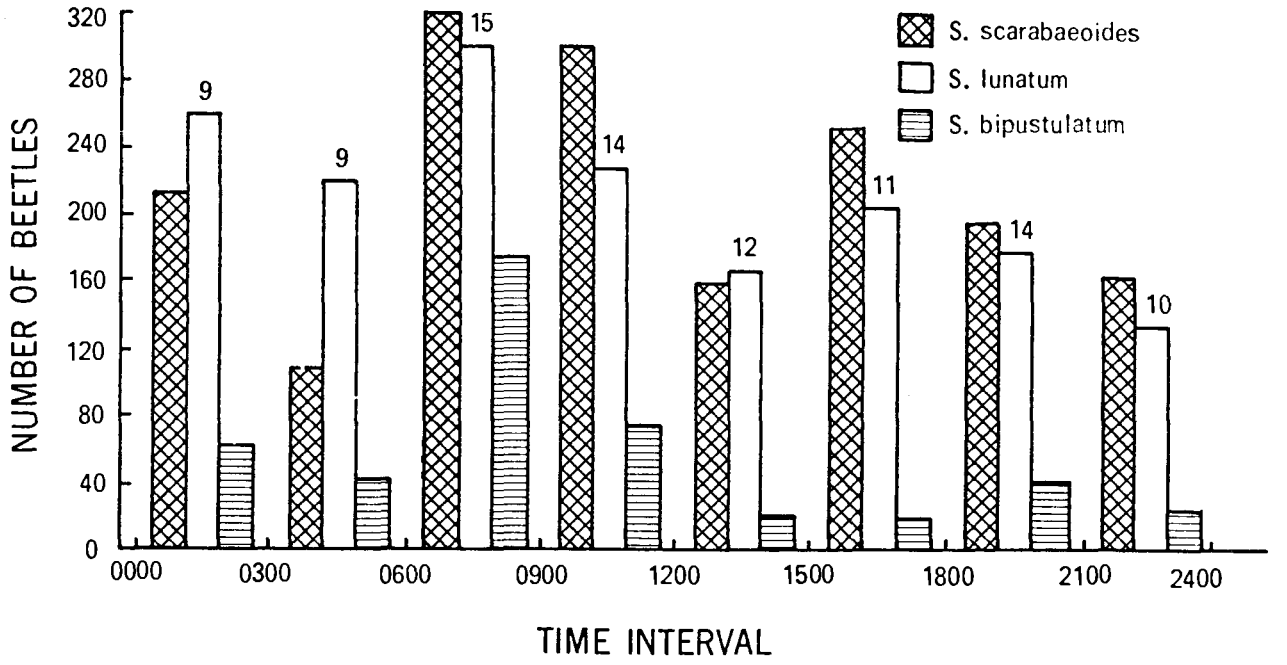
Staphylindae: Philonthus cruentatus; Aleochara bimaculata; and other less common species.

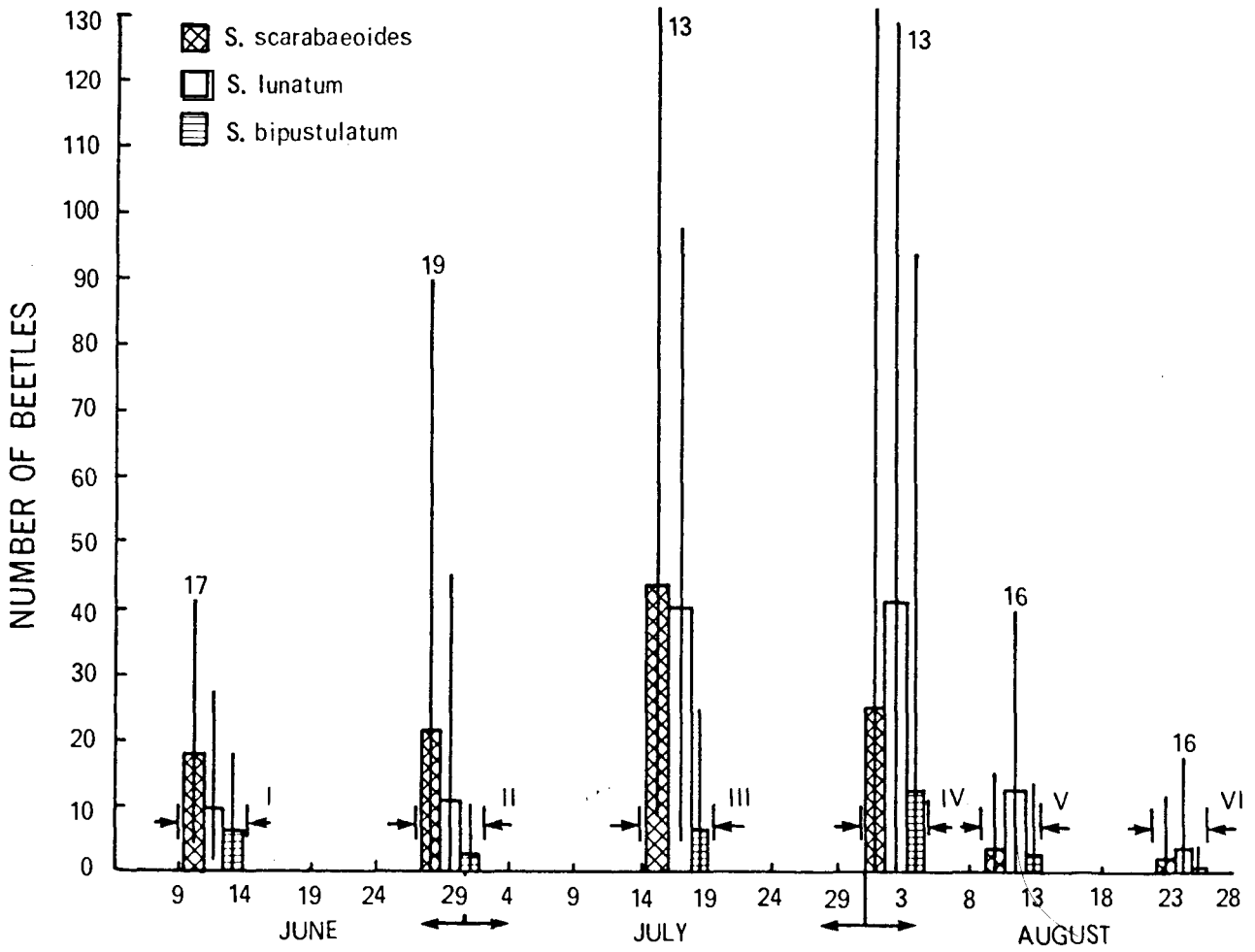
The dung-burying scarab O. nuchicornis was often present in appreciable numbers. This species did not bury dung in the greenhouse emergence cages, where the beetles had soil only about 2-3 cm deep in which to work. Normally their brood balls are buried at depths from 5-20 cm (Burmeister, 1930). Therefore the beetle could not have affected horn fly populations by removing dung from pads in the greenhouse. The remaining scarabs (Aphodiinae) probably did not affect horn fly production because they are not entomophagous and were never really abundant in pads taken from the pasture. Large numbers of Aphodiinae were observed only in the fall, at a time when there were very few other insects present in the dung. Aphodius fossor and A. fimetarius occasionally attain high numbers in the range during summer, but relatively few of these beetles occur in dung only 24 hours old.

Sphaeridium lunatum and S. scarabaeoides were by far the most prevalent species of large Hydrophilidae, both diurnally and seasonally (Figs. 16, 17). They are both of similar size, and considerably larger than S. bipustulatum. Their diurnal activity patterns are shown in Fig. 20. The Sphaeridium beetles feed on dung but have predaceous larvae (Mohr, 1943; Poorbaugh, 1966; Sanders and Dobson, 1966; Valiela, 1969) and it seemed likely that at least the two larger species may prey extensively upon horn fly larvae. S. scarabaeoides adults refused to feed on horn fly eggs or larvae in laboratory tests made in 1972. Hafez (1939) has reported rearing small S. scarabaeoides larvae through to adults on dung alone. This is a curious situation because the structure of mouth-parts suggest that the larva is a predator. Mohr (1943) recognized

Figure 16 Total number of Sphaeridium beetles taken from exposed pads in each time interval during 1971. The number of pads upon which the totals are based is given at the top of each triplet.

Figure 17 Number of Sphaeridium beetles taken from exposed pads in six successive sampling periods during 1971. For each sampling period the range of beetle numbers trapped for the three species is presented together with a mean obtained by dividing the species totals by the number of pads. The duration of each sampling period is indicated by short arrows and vertical lines above the abscissa, and the number of observations is given above each group of ranges.


S. scarabaeoides
S. lunatum
S. bipustulatum
NUMBER OF BEETLES
320
280
240
200
160
120
80
40
0
9
9
15
14
12
11
14
10
0000
0300
0600
0900
1200
1500
1800
2100
2400
TIME INTERVAL

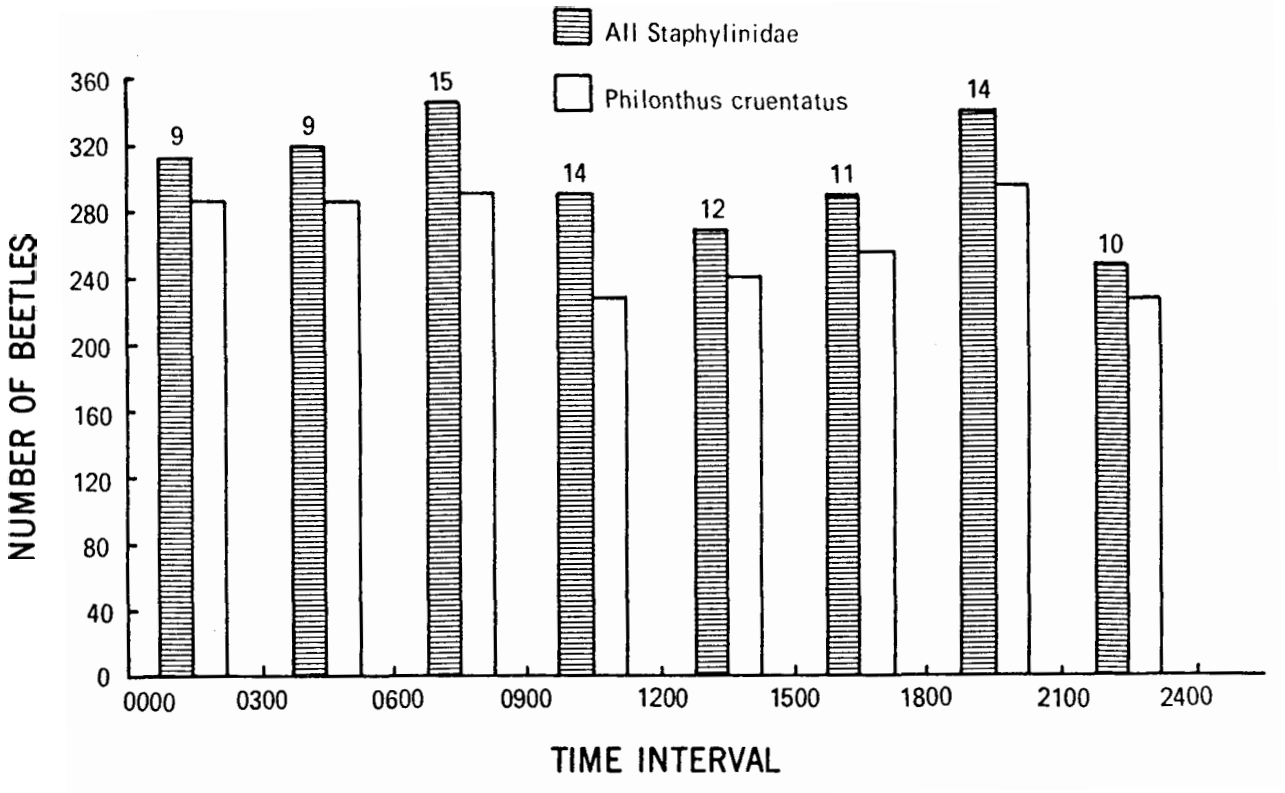

S. scarabaeoides
S. lunatum
S. bipustulatum
NUMBER OF BEETLES
130
120
110
100
90
80
70
60
50
40
30
20
10
0
17
19
13
13
16
16
I
II
III
IV
V
VI
9
14
19
24
29
4
9
14
19
24
29
3
8
13
18
23
28
JUNE
JULY
AUGUST

S. bipustulatum as belonging to a later stage in the succession; that is, the larvae are still quite young when they are left isolated by the pupation of the fast-maturing muscoid flies. This observation coupled with the low numbers of S. bipustulatum encountered suggests that the species could not have had an important effect as a predator of horn fly.

Philonthus cruentatus, a voracious predator on fly eggs and larvae, was the most abundant species of Staphylinidae. It was present in 92 out of 93 exposed samples in 1971, and was a conspicuous inhabitant of pads dropped at any time of the day, when these were collected and caged 24 hours later (Fig. 18). During 1971 this species comprised an average of 86.2% (range 73-95%) of the Staphylindae taken during the six sampling periods (Fig. 19). The species was active throughout all daylight hours except for a period in the early mornings after daybreak (Fig. 20), when temperatures were low. Relative seasonal fluctuations in its numbers (Fig. 19) were not as wide as those of the Sphaeridium species (Fig. 17). Moreover, the numbers of P. cruentatus did not show a marked decreasing trend after the end of July when the three Sphaeridium species had almost disappeared. Considerable mortality of horn fly progeny was still evident in August after the numbers of Sphaeridium had declined (Figs. 15, 17, sampling periods V and VI). This suggested, at least circumstantially, that P. cruentatus was responsible for much of the horn fly suppression. Also, because P. cruentatus is unable to burrow in dung and therefore depends on the activities of burrowing beetles (Hydrophilidae or Scarabaeidae) for access to the interior of pads (Mohr, 1943; Valiela, 1969) wherein larvae congregate, the adult staphylinids probably were able to feed only upon the horn fly eggs and freshly hatched larvae.

Figure 18 Total number of staphylinid beetles taken from exposed pads in each time interval during 1971 compared with the corresponding numbers of the most prevalent species, Philonthus cruentatus. The number of pads upon which the totals are based is given at the top of each pair of bars.

Figure 19 Number of staphylinid beetles taken from exposed pads dropped in six successive sampling periods during 1971. For each sampling period the range of total numbers of staphylinids found in pads is compared with the corresponding numbers of Philonthus cruentatus. Means were calculated by dividing the totals by the number of pads. The duration of each sampling period is indicated by short arrows and vertical lines above the abscissa, and the number of observations is given above each pair of ranges.


All Staphylinidae
Philonthus cruentatus
NUMBER OF BEETLES
360
320
280
240
200
160
120
80
40
0
9
9
15
14
12
11
14
10
0000
0300
0600
0900
1200
1500
1800
2100
2400
TIME INTERVAL

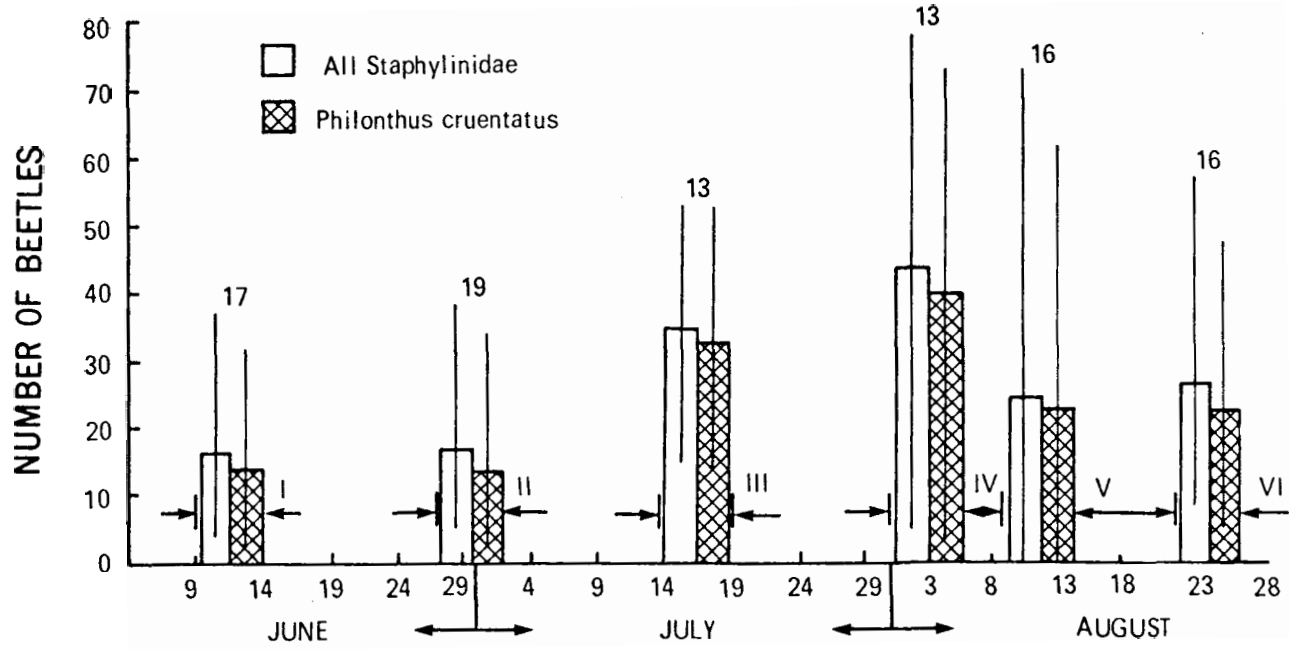
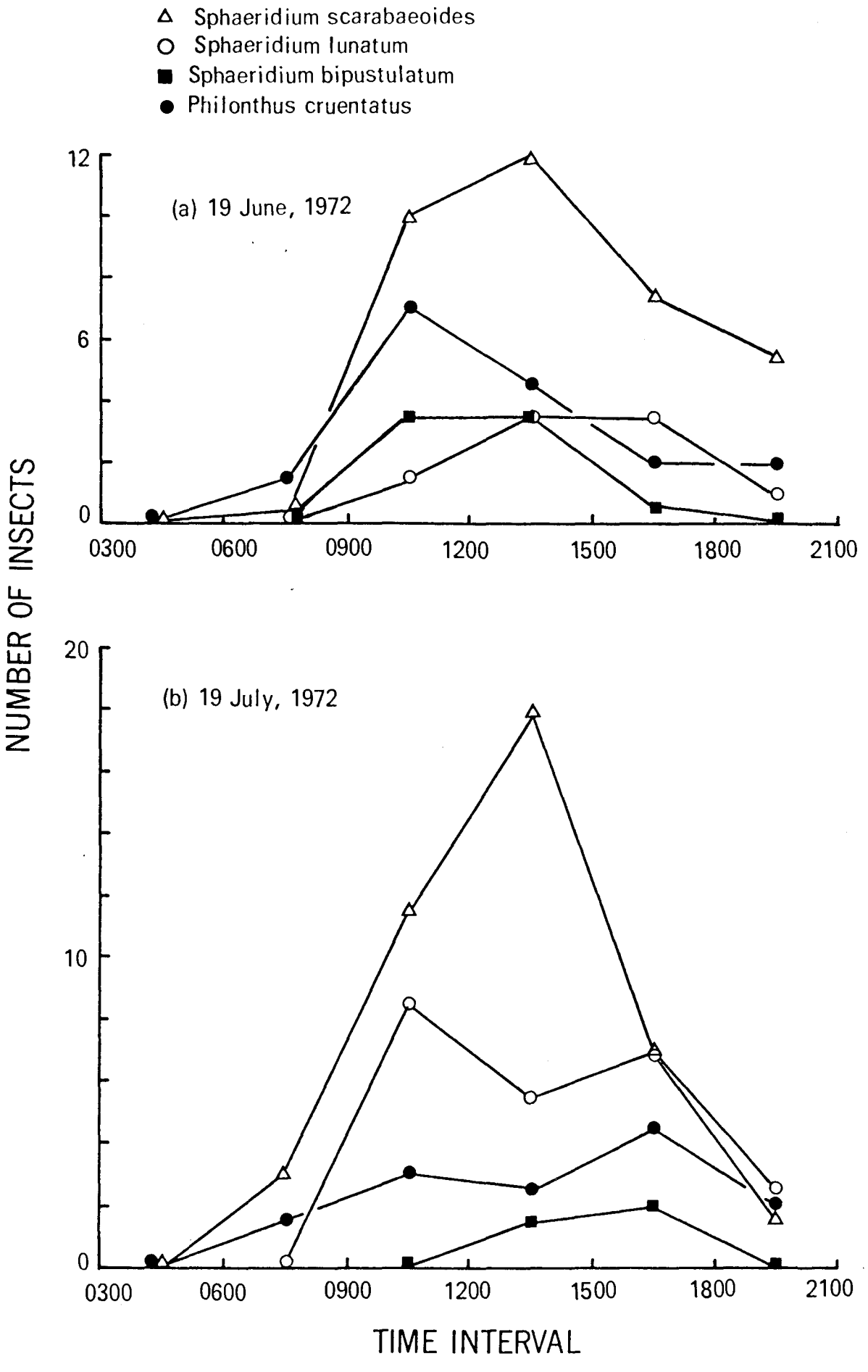

All Staphylinidae
Philonthus cruentatus
NUMBER OF BEETLES
80
70
60
50
40
30
20
10
0
17
19
13
13
16
16
I
II
III
IV
V
VI
9
14
19
24
29
4
9
14
19
24
29
3
8
13
18
23
28
JUNE
JULY
AUGUST

Figure 20 Diurnal activity patterns of some predaceous insects at Kamloops as measured by the catch of sticky traps on fresh dung pads. Data shown are the means of the catches at two pads in each time interval.


△ Sphaeridium scarabaeoides
○ Sphaeridium lunatum
■ Sphaeridium bipustulatum
● Philonthus cruentatus
(a) 19 June, 1972
(b) 19 July, 1972
NUMBER OF INSECTS
TIME INTERVAL
0
6
12
10
20
0300
0600
0900
1200
1500
1800
2100

The most common staphylinid beetle after P. cruentatus was Aleochara bimaculata. The adult of this species readily consumed eggs and small larvae of horn fly and house fly in the laboratory. A. bimaculata larvae are parasitoids, developing singly within puparia of certain flies. Lindquist (1936) found one horn fly puparium parasitized by A. bimaculata, but it was presumed not to attack horn fly normally because the adult beetles are larger than the fly and thus their larvae would be unlikely to complete normal feeding within horn fly puparia. Several A. bimaculata adults were bred from the much larger Ravinia puparia.

Myospila meditabunda is a muscid fly that is known to have predaceous larvae. Adults were bred from pads occasionally, but they were not common about the irrigated pasture, or in the open range, and it seems unlikely that the species was having a depressant effect on horn fly numbers. Hammer (1941) and Poorbaugh et al. (1968) observed that M. meditabunda cannot tolerate high temperatures and prefers droppings in shaded situations for oviposition. No other predator was present that could have taken a significant toll of horn fly.

The activity pattern of the predaceous beetles (Fig. 20) showed that irrespective of the time of pad deposition, there were always at least a few hours of exposure of unhatched horn fly eggs to P. cruentatus. For example, if a pad were dropped at 2100, by which time predator movement has normally ceased, horn fly eggs would be present on it at least until noon on the following day, allowing plenty of time for predator activity in and around the pad. Similarly, pads dropped at night are still sufficiently fresh on the following morning to be colonized and tunnelled by Sphaeridium adults. It is not known whether this species oviposits in dung that has cooled and consequently if the larvae develop in pads voided

during the night.

Field observations on P. cruentatus also lent weight to the view that it might be a major predator of the horn fly. When the weather is warm, P. cruentatus is amongst the first insects to arrive at the dropping. The beetles are very active and it was noted that often several arrived at a fresh pad before most of the ovipositing horn flies had left. On one occasion two P. cruentatus adults were observed killing and partially eating a gravid female horn fly beneath a fresh dung pad. Voris (1936) observed the beetles making similar attacks on other species of Diptera. Because the beetles are agile and some arrive as soon as a dropping is deposited, they are often in a position to attack ovipositing horn flies before these leave the pad. Even if this is a common occurrence, its actual effect on horn fly adult populations would be slight because most horn flies have left before P. cruentatus arrives in large numbers. However, the first of these beetles to arrive may disturb the horn fly females on the dung and thus interfere with oviposition.

P. cruentatus fed in the laboratory upon the eggs and larvae of house flies and horn flies. Fresh dung pads in summertime at Kamloops always supported a number of the beetles moving constantly over the surface, plucking out fly eggs or dashing into and out of tunnels made by Sphaeridium beetles. P. cruentatus also ranged over the lower side of dung pads as well as beneath them. The presence of tunnels made by burrowing beetles at Kamloops meant that P. cruentatus beetles had an opportunity to attack horn fly larvae in addition to feeding upon the eggs and adults.

The relationship between the predaceous P. cruentatus larvae and muscoid fly larvae is not known at this time. The staphylinid larvae were found in dung pads recently vacated by the muscoids, suggesting that other

species coming later in the succession form the bulk of their food.

Field experiment with Philonthus cruentatus: The above observations suggested that P. cruentatus may take a heavy toll of horn fly eggs in the 15-18 hours before they hatch. To see if this occurred, a small field experiment was conducted from 0900-1300 in July 1972 involving the caging of P. cruentatus adults with freshly voided dung upon which a known number of horn flies had oviposited. The staphylinids in the absence of burrowing beetles were probably able to prey only upon the eggs or very early larval stages of horn fly, because once the hatched larvae entered the dung the beetles would be unable to reach them.

Four pads were each covered after horn fly oviposition and then treated with 20 pairs of P. cruentatus beetles, as described in Materials and Methods (e). This number of beetles was chosen on the basis of average numbers of this species found in pads 24 hours old at that time of year. Four pads were covered but left untreated to estimate their horn fly production (controls). Pads were left in the field for 48 hours.

Horn fly production from the pads (mean number of progeny per female and range) was 2.5 (0.3-3.6) for those containing P. cruentatus and 3.0 (2.1-4.5) for the controls. No suppression of horn fly occurred. The yield of horn fly progeny from the control pads was uniformly very low. Figures obtained previously for progeny production per female between 0900-1500 hours showed that at least 4.0 and possibly 5.0 or more progeny per female could have been expected from covered pads.

Field experiment with Philonthus cruentatus and Sphaeridium scarabaeoides: Further evidence of the effect of P. cruentatus on horn fly production was sought in another field experiment conducted in early August 1972, from 0900-1500 hours. This also was designed to assess the effect of Sphaeridium scarabaeoides and the combined effect of S. scarabaeoides and P. cruentatus on the horn fly, after the fashion of an experiment described by Valiela (1969) with Musca autumnalis in New York State.

The Herefords were not available for this experiment so a herd of about 25 Jersey cows and heifers was used. Methods of the previous P. cruentatus experiment were used again. The following treatments were applied in succession to fresh dung pads after female horn flies had completed oviposition.

1. 20 Philonthus cruentatus (8 males, 12 females)
2. 20 Sphaeridium scarabaeoides (10 males, 10 females)
3. 20 P. cruentatus plus 20 S. scarabaeoides
4. No predators (control)

Three replicates of each treatment were used. Insufficient P. cruentatus males were available to balance the sexes equally. Pads were left in the field for six days before removal to the greenhouse to await horn fly emergence, to allow time for both types of predators to interact with the horn fly.

Table III shows the effect of the various predation treatments on horn fly production. An anova was performed on number of progeny per female. Significant differences between means were found by Tukey's method of multiple comparisons (Scheffe, 1959). The number of progeny produced per female was exceptionally high in the control treatment for this time of the day. P. cruentatus alone (treatment 1) caused an apparent reduction in

Table III The effect of various predation treatments on the production of horn fly progeny from naturally-voided dung pads in the field. Three replicates of each treatment were used.

Treatment	Number of progeny produced per female Mean*	Range	Progeny production as % of control
1) 20 *P. cruentatus*	6.7 a	0.8-11.2	51
2) 20 *S. scarabaeoides*	2.5 b	2.0-2.8	19
3) 20 *P. cruentatus* + 20 *S. scarabaeoides*	3.1 b	0.8-4.4	24
4) No predators (control)	13.1 a	7.6-17.7	

* Treatments sharing the same letter are not significantly different at the 5% level.

Table IV The effect of various predation treatments on the production of horn fly progeny from 250-g artificial dung pads in the greenhouse. Four replicates of each treatment were used. Each replicate initially received 100 eggs.

Treatment	Number of horn flies emerged from 100 eggs Mean*	Range	Progeny production as % of control
1) 20 *P. cruentatus*	0.8 b	0-2	1
2) 20 *S. scarabaeoides*	50.0 a	11-74	72
3) 20 *P. cruentatus* + 20 *S. scarabaeoides*	10.5 b	0-33	15
4) No predators (control)	69.8 a	65-74	

* Treatments sharing the same letter are not significantly different at the 5% level.

horn fly production in only one replicate of three. This effect may also have been caused by a low degree of horn fly oviposition in this replicate. S. scarabaeoides (treatment 2) caused the greatest and most uniform reduction, but this was not different from treatment 3 in which the two species of predator were combined. The results showed that P. cruentatus was having an erratic effect or no effect at all on horn fly under the conditions of the experiment. No interaction was observed between the two species in their effect on horn fly.

Greenhouse experiment with Philonthus cruentatus and Sphaeridium scarabaeoides: No definite evidence of predation by P. cruentatus on immature horn fly stages was obtained in the two field predation experiments. There was a possibility that this predator may have been unduly influenced by crowding or by other conditions under the mesh covers including the nature of the ground upon which the dung rested. It was impossible to keep the latter uniform; it ranged in both experiments from almost bare soil to a full grass cover, depending on defecation site. Field observations at Kamloops suggest that dung deposited in grassy locations affords a more favourable habitat for insects.

Another predation experiment in which there was greater control of such factors was established in the greenhouse later in August 1972. The same treatments were used as in the previous experiment, utilizing 250-g artificial dung pads. Ten pairs of each beetle species were used. Each treatment was replicated four times. One hundred freshly laid horn fly eggs obtained by the method of Depner (1962) were placed on each dung pad with a camel hair brush. It was impossible to place eggs underneath the pads, in the manner of normal horn fly oviposition. Instead, 20 eggs were distributed on the top surface of the pad and 80 around the sides.

The results are given in Table IV. In treatment 1 P. cruentatus caused a very low emergence (and hence almost total mortality) of the horn fly, presumably by egg predation. This is double the mortality recorded for the same treatment in the previous field experiment, and represents a greater degree of mortality than normally occurs in the field when all other insects are present. S. scarabaeoides (treatment 2) did not cause the same amount of horn fly mortality in this experiment as it did in the field (see Table III). An examination of emergence figures showed that horn fly production in this treatment was lower than that of the controls in only two of the four replicates. When the two species of predator were allowed to act together (treatment 3) in the greenhouse, horn fly mortality was generally high but the reliability of the results is in question because of lower mortality in one replicate. Opposing evidence was thus provided by the field and laboratory experiments: in the field, S. scarabaeoides appeared to be the most important predator while P. cruentatus had an indeterminate effect, and in the greenhouse the position was reversed. No time was available to investigate these relationships further.

DISCUSSION

Appendix I lists the most prominent insects associated with cattle dung at Kamloops. Many of these species were originally introduced accidentally from either Europe or Asia. Lindroth (1957) recognized the European origin of a number of insects associated with cattle dung on the east coast of North America. Most have spread progressively across to the west coast after introduction (Poorbaugh et al., 1968), although there have

been occasional separate western introductions as in the case of Onthophagus nuchicornis (Howden and Cartwright, 1963; Howden, 1966). Poorbaugh et al. (1968) listed the insect species associated with relatively fresh cattle dung in coastal California. The Californian and British Columbian dung faunas are apparently quite similar. Comparison of the west coast fauna with that associated with cattle dung in Indiana (Sanders and Dobson, 1966) and Texas (Blume, 1970) shows differences associated mainly with the Coleoptera.

At Kamloops many of the conspicuous dung insects have been introduced. The three Sphaeridium species and Onthophagus nuchicornis (Brown, 1940; Hatch, 1953), Aphodius fimetarius, A. fossor, and some of the smaller Aphodiinae (Hatch, 1953; Ritcher, 1966), Aleochara bimaculata and Philonthus cruentatus (Hatch, 1953) are all exotic. The most prevalent coprophagous muscoid Diptera at Kamloops include Haematobia irritans, Musca autumnalis, Orthellia caesarion, Ravina l'herminieri, and R. querula. The first two are definitely exotic, O. caesarion is almost certainly exotic (J.R. Vockeroth, personal communication) and the two Ravinia species are native.

The general spread of cattle throughout much of North America has afforded a means for establishment of many introduced bucoprophilous insect species; i.e., those attracted to cattle dung. Similarly, some indigenous species may have been able to expand their original ranges. In the Southern Interior of British Columbia, the assessment of insect origins listed in Appendix I shows that about 50% of the Coleoptera and Diptera are known or thought to be exotic.

The result is that at Kamloops there is now quite a diverse dung fauna and because many of the species are not indigenous, it seems that the original coprophilous fauna in the area consisted of relatively few species. Many of the introduced insects that undoubtedly coexisted in Europe are now reunited under somewhat different circumstances. It is fortunate that the same lack of quarantine precautions which permitted the horn fly and the face fly to enter this continent has also tempered their pest status by allowing introduction of some of their natural enemies.

The southern portion of Canada represents the northern limits for development of prolonged and severe infestations of horn fly on this continent. The pest is thermophilic to the extent that the Canadian climate can provide it with only a relatively short activity season. At Kamloops, the mean number of horn fly females attracted to pads in successive sampling intervals in 1971 (Fig. 12) provided a relative estimate of fly abundance during the season. The main feature of Fig. 12 is the single peak in fly abundance in late July and early August, unlike the double peaks (late May and late September) described by Bruce (1964) for the horn fly in Texas, between which the population decreased during the driest and hottest months.

The horn fly showed no clear diurnal pattern in the numbers of females ovipositing on pads (Fig. 11). In many sampling periods in 1971, there was a tendency for the number of flies visiting pads to be lowest during the hours of darkness. It may be significant that during sampling period V, in which there is no such trend apparent, evening temperatures were encountered that were higher than those in any other period. During the dark period at Kamloops, progeny production of horn flies may therefore constitute a relatively small proportion of the daily total. Ambient

temperature affects horn fly activity and in the warmer parts of its range, e.g., southern USA, where evening temperatures are high during the summer for longer periods than occur at Kamloops, the flies may be more active at night. Kunz et al. (1970) in Texas found that more horn flies were produced at night from individual covered dung pads than during the day. However, they did not trap ovipositing females and thus it is not known if the increase was due to more females ovipositing, more progeny per female, or a combination of the two. They suggested that more eggs may be deposited at night during the hot midsummer weather in this region, when relatively lower temperatures and higher humidities favoured greater fly activity.

Sampling showed that suppression of horn fly caused by other insects was substantial during the three-month period of its greatest abundance at Kamloops. Predators were also abundant and there is little doubt that they were the dominant force in reducing numbers of immature horn flies. They were common before the horn fly became active in June, and one (P. cruentatus) was still present and horn fly suppression still remained high towards the end of the horn fly activity season. In addition, the main predaceous insects were active during all daylight hours except those of the very early morning, affording even the egg stage of the horn fly no chance to escape some predation.

The suppression of horn fly measured during this investigation is probably lower than that occurring under true field conditions. Dung pads in this work were removed from the field after 24 hours. It was shown (Table II) that the number of P. cruentatus adults and other Staphylinidae in a pad continued to increase for at least 48 hours after its deposition. Numbers of most other beetles increased after 24 hours, making further

horn fly mortality a virtual certainty for pads exposed in the field until the horn fly larvae pupate. The colonization of a pad by increasing numbers of Staphylinidae may require the formation of additional galleries by burrowing insects, because the staphylinids spend relatively little time in the open, preferring the tunnels and undersides of pads.

The field and laboratory experiments with P. cruentatus and S. scarabaeoides showed that both species prey extensively on horn fly under certain conditions. The extreme variability in number of horn fly progeny produced within some predator treatments indicated that not all the important factors influencing predatory behavior were taken into account.

The erratic results that were obtained with P. cruentatus in the two field predation trials may have been caused by the experimental technique. For example, the mesh enclosures or the density of beetles used may have disturbed them sufficiently to prevent normal activity. When used at a relatively high density in the greenhouse, however, the beetles demolished nearly all the hand-placed horn fly eggs; the method of egg placement may have increased their accessibility to the predator. Since this field work was completed, Thomas and Morgan (1972b) published a study which indicated that P. cruentatus is a major predator of horn fly in Missouri, especially of the egg stage.

S. scarabaeoides greatly reduced horn fly numbers in the field experiment (Table III) but did not have a similar effect in the greenhouse test (Table IV). Only the larvae of this species are predaceous. Hence experiments of this type will be affected directly by the number of gravid female beetles that are included in each replicate. It was not possible to

determine whether such females were present at the start of these experiments.

The predation experiments failed to establish whether or not an interaction occurs between P. cruentatus, S. scarabaeoides and horn fly larvae. No increased horn fly mortality occurred when both species were present in comparison with each predator acting singly. Valiela (1969) used S. scarabaeoides in an attempt to demonstrate the effect of a burrowing beetle in improving the predatory efficiency of P. cruentatus on face fly larvae. He found that the hydrophilid by itself had no significant effect on survival of face fly larvae. However, mortality of face fly was higher when both species were present than when P. cruentatus was used alone. Valiela stated that S. scarabaeoides larvae are not predators of face fly larvae and therefore attributed the increased mortality solely to the action of the burrowing Sphaeridium adults in making fly larvae more accessible to P. cruentatus. His results are based on few replicates and do not provide irrefutable evidence that at least some of this additional mortality was not caused by predation of S. scarabaeoides larvae on the face fly larvae.

If the sluggish S. scarabaeoides larvae are incapable of feeding upon even first instar face fly larvae (Valiela, 1969), the reason is more likely to lie in the bodily strength and cuticular toughness of the fly larvae rather than the slowness of the predator. Both types of larvae can move within the actual dung mass instead of depending on tunnels. It hardly seems necessary for speed of locomotion to be a prerequisite for an efficient predator in this type of medium. The S. scarabaeoides larvae need only be capable of orientating themselves into the path of moving fly larvae in order to attack them when

they come within range. S. scarabaeoides larvae have been observed preying on many different species of fly larvae (Poorbaugh et al., 1968), some larger than themselves, e.g., Cryptolucilia (now Orthellia) caesarion (Hammer, 1941) - about the size of a house fly - and even half-grown Sarcophaga (now Ravinia) l'herminieri (Mohr, 1943). The latter is one of the largest muscoid species present in dung. Horn fly larvae at maturity attain about half the size of house fly larvae. S. scarabaeoides preyed on horn fly larvae in the studies of Mohr (1943), and also during this investigation. Thomas and Morgan (1972b) considered it an important predator of horn fly. It can probably overpower all instars of the very active horn fly larvae, in view of its ability to cope with larvae of some larger species.

No mention has been made so far of Sphaeridium lunatum, a species that was present in lower numbers than S. scarabaeoides during most of the summer but that became more numerous as the numbers of the latter declined (Fig. 17). Larvae of S. lunatum are predaceous (Poorbaugh et al., 1968) but nothing is known of their activity in dung at Kamloops. Currently there is no reason to suppose that they are not general predators like S. scarabaeoides larvae, so that the horn fly larvae may form a part of their natural diet.

Numbers of all three species of Sphaeridium started to decline early in August. Hammer (1941) also observed this in Denmark, and noted a corresponding increase in numbers of the coprophagous larvae of Cryptolucilia (now Orthellia) caesarion. Were it not for the presence of P. cruentatus at Kamloops, the decrease in Sphaeridium might result in an increase in coprophagous fly breeding in the late summer.

Just as the horn fly suffers heavy mortality during its immature stages in dung, so also do the other flies associated with it.

Very seldom were large numbers of coprophagous flies bred from the exposed pads taken during the field sampling. Similar low yields of flies were obtained from pads dropped in the open range and brought to the laboratory for extraction of predators. It seems unlikely that coprophagous Diptera ever met limitations in the form of food scarcity in this area. Poorbaugh et al. (1968) regarded competition for food or space among coprophagous Diptera as being rarely, if ever, an important mortality factor. Bay, Pitts, and Ward (1970) have shown that a face fly larva requires 2.0 g of fresh feces for normal larval development. No equivalent figures are available for the horn fly but it is likely to be approximately 1.0 - 1.5 g; for O. caesarion, about 2.0 g and for the large Sarcophagidae, possibly 4.0 g. Comparison of these figures with the mean adult emergence figures showed that only a small amount of the food available for coprophagous flies was actually converted into adult tissues, because an average pad (2,000 g) would have the potential to produce several hundred flies. Some of the nutrients in the pad are converted into predator tissue, but less loss would occur from this than if the flies were able to develop free of predation. Valiela (1969) considered that most of the predation probably occurs in the egg and early larval stages for the larger dipterous species, because as these develop they eventually become too large for most predators to handle. The predators thus may be performing another service in addition to the destruction of pest flies: in destroying other immature Diptera they are also preventing some loss of dung nutrients in the form of insect tissue, as well as any other nutrient losses (e.g., nitrogen) that may result from concentrated insect activity in dung pads.

It was mentioned earlier that exposed pads had to be protected with frames against bird attack. Bird activity was sporadic during most of the summer, but as Valiela (1969) has observed, the scattering of a dung pad by bird action has a catastrophic effect on the insect inhabitants of any one dropping. It was therefore necessary to protect all the experimental pads to avoid losing any of them. Many unprotected pads were torn to pieces by birds (mainly starlings and cowbirds) in late summer and it is likely that numbers of overwintering horn fly puparia were thereby reduced.

Anderson (1966), noting that insects are especially important in converting feces to arthropod biomass, considered that the action of coprophagous flies in pasture is beneficial in the sense that they actually remove much of the energy and organic load from cattle droppings. In summer pasture conditions in California, he noted that most of a cow pad can "fly away" in 2-3 weeks. Papp (1970) also found that the presence of many fly larvae in cow dung facilitates the breakdown process. Although the transfer and uptake of dung nutrients and disintegration of pads during the presence of these insects may appear to be beneficial from the standpoint of anyone interested in dung removal per se, the fact remains that under such conditions nutrients are being lost or tied up in insect tissue unnecessarily. Better economy of nutrients could be achieved by utilizing the activity of dung beetles.

It is evident that the stages of the horn fly most vulnerable to natural enemies are the immature ones. These are concentrated in or near a relatively small volume of food medium which is also attractive to a large number of other insects. Through introduction of dung beetles and perhaps predators from other areas it may be possible to create conditions

for immature horn flies that are less favourable than they are now. Moreover, better dung disposal might be effected than occurs at present. The horn fly and its host have Old World origins and moreover there is a marked discontinuity in indigenous dung insect faunas that is apparent between the New and Old Worlds. It is my opinion that research with biological manipulation of cattle dung and its insect fauna as the objective will ultimately yield the most satisfactory solution to the problems that have been created.

CHAPTER II - DUNG BURIAL ACTIVITY OF ONTHOPHAGUS NUCHICORNIS

INTRODUCTION

Currently there are only two species of dung-burying beetles in the rangelands of the Southern Interior of British Columbia. One of these, Boreocanthon simplex LeConte, is native and was rarely taken during this investigation. The other beetle is Onthophagus nuchicornis (Linnaeus), introduced separately from Europe to both the east (Brown, 1940) and west coasts of North America (Howden, 1966). The first record of this species in British Columbia was from Creston in 1945 (Hatch, 1971). Since that time it has effectively colonized the southern portion of the Province, being present in the Interior and also in the humid lower mainland area surrounding Vancouver. According to Balthasar (1963b), O. nuchicornis is found in every part of Europe with the exception of the most northerly regions, and also in Asia Minor, the Caucasus, Turkestan, Siberia, and Mongolia. It thus may have the potential to colonize a greater area of western North America than it occupied in 1966, which was southern British Columbia, Washington, Idaho, and western Montana (Howden, 1966).

Its biology in Europe was described by Burmeister (1930), and additional information was provided by von Lengerken (1954). During the summers of 1971 and 1972, some observations were made on the biology of the beetle at Kamloops.

O. nuchicornis is very common in the Interior. The over-wintering beetles emerged in April and early May and began a period of feeding and dung burial which lasted until about mid-July, when the summer drought commenced. Beetles collected in late July and August failed to

bury dung even if soil was quite moist. Fresh cattle pads and also horse dung in the range often contained enormous numbers of O. nuchicornis in August, which were evidently feeding. It was not uncommon at this time for even large pads to be completely shredded and dispersed by the beetles. While little or none of the dung was buried, the churning action of the beetles should have facilitated its breakdown. The fate of fly larvae attempting to develop in such pads is not known for certain. Nothing is known of the habits of the beetles from the time cooler weather comes to the Interior (usually late August) until winter arrives, except that they diapause in the adult stage. The active period in spring and early summer would theoretically allow time for two generations to develop, because the time required for an egg in a brood ball to mature into an adult varied from about five to nearly eight weeks. Probably no further generations occur in the fall and the species may in fact be univoltine. The large numbers of beetles present in August may represent a peak in emergence of the generation derived from the original overwintering parents, and these progeny then become concentrated in the relatively few available dung pads.

The horn fly field sampling procedures described in Chapter I did not yield any information about O. nuchicornis apart from the numbers present in each pad, which led to an estimate of seasonal abundance. During the sampling it proved impossible to obtain any estimate of the potential of the beetles for dung burial. Field observations suggested that dung removal occurred to the extent where it could interfere with fly breeding only if the pads were small and fairly shallow. Therefore the activities and effectiveness of this beetle were investigated in the

greenhouse and the results were supported by field observations, the better to judge if importation of other beetle species would be worthwhile to increase the amount of dung disposal in the field. The beetle was also employed as a dung-burying animal in various laboratory experiments.

Bornemissza (1970) demonstrated the effect of the activity of dung-burying beetles on coprophagous fly larvae sharing the same dung mass. In experiments with the horn fly in Hawaii and with the bush fly (Musca vetustissima Walker) in Australia, he showed that when moderate numbers of very efficient dung beetles colonized a pad, emergence of adult flies from it was drastically reduced or even eliminated. Moreover, the few flies emerging from experimental pads that had been subjected to a lower degree of beetle activity were small, stunted, and had little or no reproductive ability. Thus dung burial can have a pronounced harmful effect on fly populations even if it does not completely prevent development of their larvae.

Experimentation in 1971 and 1972 therefore sought to define the potential of O. nuchicornis for dung burial and the effect of such burial by this species on development of coprophagous fly larvae, particularly those of the horn fly.

MATERIALS AND METHODS

Assessment of the Potential of O. nuchicornis for Dung Burial.

Burial tests were made with artificial dung pads resting on 10 cm of soil in pots made out of cut-down three-quart milk cartons. The soil was a fine sandy loam taken from the lower grassland and dampened after potting to a moisture content of about 25%.

A herd of Hereford cows was always available at the Research Station, but their dung was seldom used for laboratory and greenhouse experiments, because the quantities of fresh dung sometimes required made field dung collection impracticable. Dung for experiments was therefore collected from the Tranquille School dairy farm near Kamloops. Large quantities of dung were available at 0400 and 1500 hours during the day.

The dairy cows were normally moved to fresh irrigated pasture every three days. This ensured a degree of standardization in the moisture content and quality of the dung throughout the summer. All animals were fed a supplementary ration of alfalfa hay at each milking time.

After collection the dung was thoroughly mixed. The standard fresh weight of pads for many experiments was 200 or 250 g. An open-ended metal trough served as a receptacle for weighing the dung, from which the mass was transferred into a cylindrical aluminum mold 9 cm in diameter that rested on soil in one of the pots. Dung was tamped into the mold before the latter was removed, leaving a neat pad 3 cm high (200 g) or 4 cm high (250 g). Two identical control pads were always prepared on small aluminum dishes and oven-dried at 100°C for moisture and dry matter determinations.

Beetles were captured in range or pasture by overturning fresh pads and searching through the dung. Surface soil beneath the pad was searched also. In the laboratory the beetles were sexed and the sexes were separated. They were held for 48 hours without food in waxed cartons containing damp facial tissues to allow for appearance of mortality caused during collection. Prior to use in an experiment they were checked for damage and given a test to make sure they were capable of normal

activity. They were then sorted to assure a uniform size of beetle in each replicate. Males and females were combined and held in jars assigned to each replicate while the rest of the experiment was prepared. Equal numbers of males and females were always used.

After dung was placed on the soil in pots, the beetles were introduced and confined with nylon mesh screen secured with rubber bands. Burial activity was indicated by the appearance of excavated soil beside and within pads. Beetles coming to the surface of pots after about five days were released.

Soil pots were dismantled at the end of the experiment. Firstly the dung remaining on the soil surface was collected. This consisted of the dry original dung mass, usually honeycombed with tunnels, some of which contained soil excavated by the beetles. It was not feasible to extract all the soil from within the dung pad. Instead, the pads containing soil as well as all dung fragments on the soil surface were removed and dried at 100°C to stop mold growth. The remains were held in individual plastic bags for subsequent determination of amount of dung burial.

The soil was then thoroughly searched for dung balls. Only completed or nearly completed brood balls were counted. Small caches of dung probably representing adult food stores were infrequently found.

The dung pads were processed by an ashing technique to determine the amount of dry dung remaining. The water flotation technique described by Bornemissza (1970) for separating soil from kangaroo dung was not used because in these experiments the soil was often packed too firmly into tunnels in the dung.

The remains of each pad plus adhering soil were placed in a crucible, dried at 100°C and then weighed. Ashing was carried out in a muffle furnace at 600°C for 24 hours. Crucibles were then brought to 100°C and weighed again. Separate determinations showed that oven-dry dung from the Tranquille dairy lost 81% of its dry weight on ashing, while range soil underwent a loss of 4%. Using these figures a simple formula was constructed (Appendix III) for calculating the amount of dung remaining, and hence unburied, on the soil surface:

Dry weight of unburied dung = (0.96 DW - AW)/0.77,

where DW is the weight of dry dung plus soil before ashing, and AW is the weight of ash plus soil.

The percentage burial on a dry weight basis for any pad was then calculated using the formula

$$\% \text{ dung buried} = \frac{100 \text{ (weight control pads - weight unburied dung)}}{\text{weight control pads}}$$

The formulae overestimated the amount of dung buried, because fresh dung invariably lost dry matter when it was exposed on a damp or dry soil surface. Drainage of dung liquid and volatilization of some constituents were probably responsible. Correction factors were found by use of control pads, and these were subtracted from the apparent per cent burial figures to give the actual amount buried.

Effect of Dung Burial by O. nuchicornis on Development of Coprophagous Fly Larvae.

O. nuchicornis is now known to bury dung until about the middle of July. The horn fly does not become numerous in the field until about mid-June. Thus only about four to six weeks were available per year when sufficient numbers of horn fly adults could be collected from cattle

to furnish an adequate supply of eggs for experiments, while at the same time O. nuchicornis was still actively burying dung. Such a short time for a simultaneous experimentation with these two species offered only a precarious chance of obtaining useful results because often about three weeks were required after the beginning of an experiment until all adult flies had emerged. To count horn fly puparia instead of emerged adults would have reduced the time lag, but this was not done because a lot of time would have been required to recover them. As only one summer was available for this work, it was decided that as a safeguard, use would be made of Musca domestica larvae as coprophagous animals for these experiments early in the season before horn fly became active. Coprophagous Diptera in the same family will have basically the same food requirements, so that an animal (i.e., dung beetle) that is competing for this food should have the same effect on all such species within the family.

House flies were reared continuously in the laboratory at Kamloops during the 1972 summer. For a beetle versus fly experiment, preparations were made exactly as described for a normal dung burial experiment. House fly eggs were collected before the experiment began, timed so that hatching into small larvae had occurred only a few hours before the start of the experiment. After pads had been prepared, 100 first instar house fly larvae were counted and transferred onto the top of the artificial pad. When all pads including controls had received larvae, beetles were released into their treatments. Different numbers of beetles were employed to provide a graded increase in the amount of dung buried without using the higher levels of beetle infestation that lead to inefficient burial. In the single experiment with house fly, four beetle treatments (1, 2, 4, and 8 pairs) were planned, replicated

five times. Just before the experiment was established it was found that half the fly larvae intended for infestation of pads had been asphyxiated, due to the formation of an airtight seal by condensed moisture at the junction of the lid and bottom of their petri dish. The number of replicates was then reduced to three.

Horn flies were collected when required by running the Hereford cattle into a stockyard and sweeping their backs with a net. Flies were induced to oviposit by using a slight modification of the method of Depner (1962). The modification involved the use of filter papers dampened with a mixture of fresh dung and water. These were placed at the bottom of 500 ml Erlenmeyer flasks containing 200-300 horn flies. Flies laid many eggs on the filter paper during exposure to 30°C for 4-5 hours in a darkened incubator, and afterwards were returned to the cattle. Eggs were rinsed out of the flasks with small portions of tap water into a Buchner funnel (Depner, 1962). Horn fly larvae are much more active than those of the house fly, and are difficult to transfer individually from place to place. Because of this, dung was infested with horn fly eggs instead of larvae.

Horn fly eggs were counted onto moistened one-inch squares of filter paper (Depner, 1961), which were then placed on the top of the pad and covered lightly with the shallow lid of a 9 cm plastic petri dish to increase humidity in the air surrounding the eggs. The experiments with horn flies were established only a few hours prior to the expected time of first hatching of the eggs. As soon as the horn fly eggs had been placed in position, beetles were liberated into their respective pots, where initially they remained beneath the pads and did not bother the hatching horn fly larvae. Pots were kept out of the sun until about 12 hours after the start of the experiment to allow sufficient time for

hatching of horn fly eggs, and then they were placed in a greenhouse. The squares of filter paper were retrieved from the dung surface later so that the number of non-viable eggs could be counted.

Beetles that left the dung and appeared in the enclosure at the top of the pots were removed periodically. Pots remained in the greenhouse until all flies had emerged and died. The same procedure was used for dismantling pots in these fly experiments as for the burial experiment. Emerged flies were collected, counted and weighed. Remains of pads were retained for estimation of per cent burial, and soil in pots was thoroughly searched for brood balls.

RESULTS

The Burial Potential of O. nuchicornis.

Several small preliminary experiments were conducted in 1971 to measure the amount of dung that was removed by various numbers of active O. nuchicornis. This information was required prior to the establishment of certain other experiments.

The first experiments suggested that maximum burial of a 200-g pad was obtained when four or five pairs of beetles were present. Below that number, fewer brood balls were recovered from the soil, while the number of brood balls decreased again as the number of pairs of beetles increased above five, implying that interference with burial was occurring at what were probably unnaturally high beetle densities. In one early experiment, 5 pairs of beetles (10 replicates) buried an average of 27.5 dung balls per pot and in doing so removed 37.4% of the original 200 g of fresh dung, for a calculated dry matter weight per dung ball of 0.37 g.

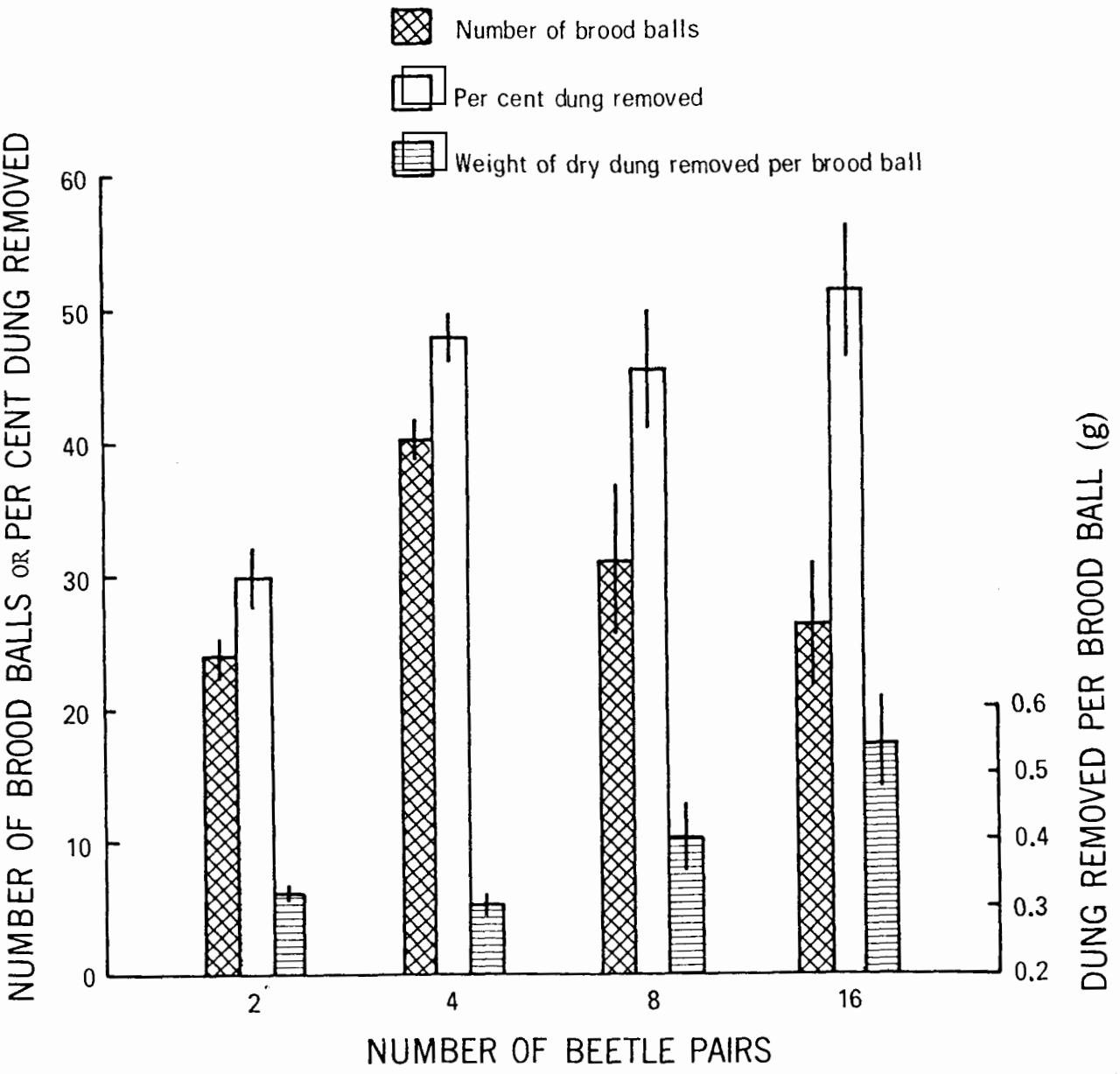
A similar but larger experiment was conducted in mid-July 1971 to establish firmer guidelines for greenhouse evaluation of the effect of beetles on the breeding of coprophagous flies. In this experiment, treatments consisted of 2, 4, 8, or 16 pairs of beetles per 200-g pad, replicated four times. In some replicates no dung was buried, and in most of the others burial activity was much reduced. Tests throughout the remainder of the 1971 summer until the end of August showed a complete lack of burial activity. It was thus impossible either to examine beetle burial activity further for the remainder of the 1971 research season, or to conduct any experiments with beetles and coprophagous fly larvae.

In May 1972 a definitive experiment was established to evaluate burial of dung by O. nuchicornis, which is very active at this time of year. Treatments of 2, 4, 8, or 16 pairs of beetles were used as in 1971, with five replications. The results are shown in Fig. 21.

The number of brood balls recovered per pot rose from 23.6 at a density of 2 pairs of beetles to 40.2 for 4 pairs (a 70% increase). Thereafter the number of balls declined as the number of beetles increased, indicating that at high densities mutual interference prevents some breeding pairs from initiating brood ball construction, or reduces the number of brood balls produced per breeding pair. Beetles are not found in field pads during the breeding season in numbers representing the two higher densities used, though, as has already been mentioned, tremendous numbers of non-breeding beetles occur in pads later in the summer.

Four pairs of beetles removed about 60% more dung from the surface than two pairs (i.e., 47.6% burial compared with 29.6%), which is fairly consistent with the 70% increase in number of brood balls

Figure 21 Dung burial activity by various numbers of Onthophagus nuchicornis beetle pairs provided with 200 g of fresh dung. Values indicated are means of 5 replicates and vertical lines represent standard errors.


Number of brood balls
Per cent dung removed
Weight of dry dung removed per brood ball
NUMBER OF BROOD BALLS OR PER CENT DUNG REMOVED
DUNG REMOVED PER BROOD BALL (g)
60
50
40
30
20
10
0
0.6
0.5
0.4
0.3
0.2
2
4
8
16
NUMBER OF BEETLE PAIRS

mentioned above. However, in the treatment using 8 pairs, even though the number of dung balls declined to 31, the amount of dung removed was approximately the same as for 4 pairs. Sixteen pairs of beetles buried only 26.2 brood balls but in spite of this they removed at least as much dung as did 4 or 8 pairs.

Calculation of the amount of dry dung removed per brood ball recovered showed no significant difference (by a t-test) between the means for 2 and 4 pairs of beetles (0.32g and 0.30 g respectively). Regression of per cent dung removed on number of brood balls buried by 2 or 4 pairs of beetles showed a highly significant relationship ($N=10$; $Y=4.14 + 1.08X$; $r=0.961$; $P<0.001$). The number of brood balls recovered therefore was a direct indication of the amount of burial activity in each pot. For these treatments, the mean amount of dung removed per brood ball probably indicates the basic dung utilization per breeding pair and includes the dung consumed by beetles as well as that incorporated into brood balls. The figures of 0.30 and 0.32 g dry dung per brood ball recovered agree closely with the estimate of 0.37 g mentioned for an earlier experiment, and represent a total removal of approximately 2.5 g of fresh dung for each brood ball.

Dung removed per brood ball buried by 8 pairs of beetles was greater ($P<0.05$) than that removed by 4 pairs but not significantly different from that removed by 2 pairs. Dung removed per brood ball buried by 16 pairs of beetles was significantly greater ($P<0.01$) than the amount removed by 2 or 4 pairs, but not by 8 pairs. These figures show that at the two higher beetle densities, the insects removed considerably more dung from the pad than was actually packed into brood balls. The missing dung presumably was either consumed by beetles or taken by them into the soil in small quantities which were not noticeable when the soil was searched for brood balls. These extraneous losses tended to increase

in relation to the number of beetles present and appeared to be highest in the treatment using 16 pairs of beetles.

Effect of Dung Burial on Development of Coprophagous Fly Larvae.

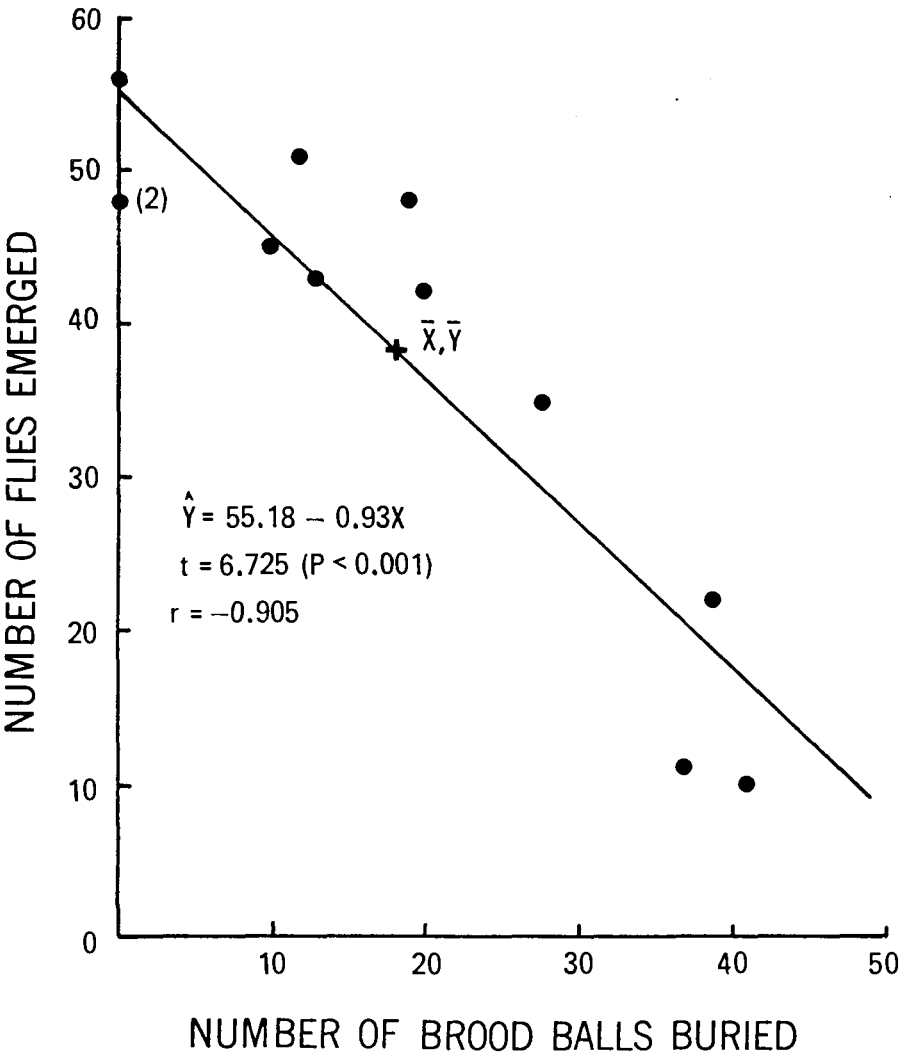
The first test to examine the effect of dung burial by O. nuchicornis on fly development commenced on 1 June, 1972, using house fly larvae. Treatments used involved a control and 2, 4, and 6 pairs of beetles respectively.

Dung removal at these beetle densities again bore a highly significant relationship to the number of brood balls formed ($N=12$; $Y=14.02 + 0.88X$; $r=0.985$; $P<0.001$). The regression of number of house flies surviving on number of brood balls formed showed a highly significant inverse relationship between the two (Fig. 22). Under the conditions of this experiment, fly survival fell as dung removal by beetles increased.

Survival of house flies in the three replicates of the control treatment was uniformly low; a mean number of 51 adults was produced from the original 100 first instar larvae. Subsequent small trials with different numbers of house fly larvae in the same quantity of dung suggested that even though each larva in the experiment initially had 2.5 g of dung, the rapid drying of such small pads soon introduced competition for food and lowered survival. Bay, Pitts, and Ward (1970) showed that the larvae of a similar-sized fly, Musca autumnalis, require about 2.0 g of fresh dung for optimum development, but it appears that the dung in their experiments was not subjected to dehydrating conditions caused by sun in the greenhouse and liquid absorption by soil.

It has been shown that dung burial by O. nuchicornis reduced survival of house fly larvae if these were sufficiently numerous to be

Figure 22 Regression of number of house fly larvae that reached the adult stage on the number of brood balls buried by Onthophagus nuchicornis in each pot. Each pad contained 100 larvae at the start of the experiment. Pads from which no brood balls were buried contained no beetles.


60
50
40
30
20
10
0
(2)
$\bar{X},\bar{Y}$
$\hat{Y}$ = 55.18 – 0.93X
t = 6.725 (P < 0.001)
r = –0.905
10
20
30
40
50
NUMBER OF FLIES EMERGED
NUMBER OF BROOD BALLS BURIED

competing for food and space even in the absence of beetles. In this work the actual performance of the beetle was as much under scrutiny as its ability to influence the survival of coprophagous Diptera. Therefore it was of interest to measure the effect of its dung burial efforts on development of fly larvae when these were present in numbers approximating some field infestations.

When horn fly adults became plentiful in the field, two experiments were established that were similar to the one just described. Each employed beetles in four treatments including a control and was replicated five times. Fifty-five eggs were placed on dung in each pot. Based on laboratory measurements of per cent hatch at that time, this number of eggs was calculated to yield approximately 50 larvae, which in 250 g dung pads represented a density of horn fly larvae that would seldom be exceeded in the field.

No correlation was found between number of horn flies that emerged and the number of brood balls buried in each pot. The results of the two experiments were then subjected to anovas and are presented in Table V. Dung burial by beetles had no evident effect on the survival of the horn fly larvae. Absence of competition for food between larvae in the beetle treatments was indicated by the mean body weight of adult flies, which was equal to or greater than that of flies in the controls. These results suggest that when horn fly larvae are present in the density that was used, a large proportion of the dung mass containing them would have to be removed in order to affect their survival seriously.

During August O. nuchicornis adults are mostly found tunnelling within dung but not burying it. This period coincides with that of greatest horn fly abundance (Fig. 1). Another experiment was established to obtain information on the effect of tunnelling and feeding by the non-burying beetles on the development of horn fly.

Table V The effect of dung burial by Onthophagus nuchicornis on the survival of horn fly larvae. Figures given are means or means ± SE.

Pairs of beetles (treatments)*	Number of brood balls	% loss in dung dry weight	Calculated % dung buried	% survival of horn fly**	Weight of horn fly adult (mg)**
		EXPERIMENT 1: 27 June, 1972			
0	---	14.1	---	64.5 ± 10.3 a	0.58 ± 0.03 a
2	20.0 ± 2.6	29.9	15.8	80.9 ± 5.2 a	0.70 ± 0.02 b
4	28.4 ± 1.2	38.2	24.1	65.2 ± 10.4 a	0.70 ± 0.03 b
8	37.2 ± 3.4	48.2	34.1	76.0 ± 6.0 a	0.69 ± 0.03 ab
		EXPERIMENT 2: 5 July, 1972			
0	---	16.2	---	74.0 ± 0.2 a	0.70 ± 0.02 a
2	18.0 ± 2.0	30.9	14.7	73.8 ± 5.3 a	0.76 ± 0.02 a
3	26.4 ± 3.7	34.7	18.5	73.4 ± 5.1 a	0.76 ± 0.01 a
4	24.4 ± 2.9	31.8	15.6	65.4 ± 5.4 a	0.76 ± 0.02 a

* 5 replicates in all treatments; 55 eggs per replicate; mean hatch was 83.9 %.

** Means sharing the same letter are not significantly different at the 5% level; percentages transformed to arcsine for statistical treatment.

The same procedures were used as in the previous experiments. Four beetle treatments were used (0, 4, 8, 16 pairs), each replicated three times. High numbers of horn flies were used (200 eggs/250 g pad).

No brood balls were buried (Table VI). An anova showed no difference between treatments for either per cent survival or mean weight of horn fly adults. A trend of increasing loss of dung dry weight is evident as the number of beetles was increased. Dung at beetle densities of 8 and 16 pairs was thoroughly tunnelled and pads were more flattened in comparison with those that contained lower densities. Relatively high numbers of non-burying O. nuchicornis therefore did not affect horn fly survival in pads even when the latter were abundant (i.e., 181 larvae in 250 g dung). This indicates that it is only the dung burial activity of beetles which may have detrimental effects on development of coprophagous fly larvae.

DISCUSSION

The experiment with house fly larvae (Fig. 22) showed that under certain conditions, survival of fly larvae in dung decreased as the amount of dung buried increased. The amount buried and the speed at which it is buried are important in preventing the development of fly larvae. Bornemissza (1970) working with the very efficient dung beetle O. gazella Fabricius and the bush fly showed that when dung pads were colonized by beetles that were capable of utilizing all the feces, survival of the coprophagous fly larvae was related to the speed of burial. O. gazella, even at the lowest density used (1 pair/100 cm^3 of dung), removed most or all of the dung within 48 hours. Increasing the number of beetles in a pad thus directly increased the speed of burial, permitting an examination of

Table VI The effect of various numbers of non-burying Onthophagus nuchicornis on the survival of horn fly larvae. Figures given are means or means ± SE.

Pairs of beetles (treatments)*	% loss in dung dry weight	% survival of horn fly**	Weight of horn fly adult (mg)**
0	14.4	73.7±10.3	0.58±0.01
4	17.5	69.0± 0.4	0.65±0.02
8	19.5	72.6± 2.7	0.61±0.01
16	21.5	66.8± 0.1	0.59±0.02

* 3 replicates per treatment; 200 eggs per replicate; mean hatch was 90.4%.

** No significant differences between treatments; percentages transformed to arcsine for statistical treatment.

this effect alone.

In the house fly experiment, O. nuchicornis was not capable of utilizing the whole pad. Beetle density in dung ranged from 1 pair/125 cm^3 to 1 pair/41 cm^3 and burial ranged from about 7 to 40% respectively. Thus an increase in beetle number increased both the total amount of dung buried and the speed of removal, producing an interaction in which it is impossible to separate the two component effects.

While the experiments involving beetles and horn fly did not support the demonstrated trend of suppression by beetles on house fly, results obtained helped to evaluate the performance of O. nuchicornis. In the first two experiments with horn fly larval density representing a high level of field infestation (i.e., 55 eggs/250 g dung),it is apparent that there was still plenty of food available for the larvae, even after burial of 34% of the dung mass (Table V, experiment 1, 8 pairs of beetles).

There are two possible alternatives to be assessed when considering the field implications of these results:

- that fly larvae are present in field pads in sufficient numbers to be forced automatically into competition for food, in which case any dung burial is likely to affect their survival, or
- that O. nuchicornis buries sufficient dung in the field to force the coprophagous larvae into severe competition with each other.

Neither alternative appears to be likely. Firstly, in Chapter I, I concluded that dung pads on Kamloops range apparently are

under-utilized by coprophagous Diptera, on the basis of the small numbers of normal-sized flies which usually emerged from pads in relation to the amount of food actually present. Poorbaugh et al. (1968) made a similar deduction in California. Responsibility for this can be attributed to the effective complex of predators, which crop the immature coprophages, including horn fly, reducing their numbers and the chances of establishing competition between them for food.

Secondly, the results of the foregoing experiments show that O. nuchicornis is a dung burier of limited worth. Observations in the field indicated that the beetle has very little impact on large pads except during its midsummer period of intensive but non-burying colonization of dung. However, in spring and early summer any small (250-500 g) thin pads, such as are made by cattle defecating while walking slowly, may be almost entirely removed except for their hardened crust. This activity is very noticeable after showers of rain. Field evidence is obviously the best indication of the true potential for dung burial.

This degree of dung burial from small pads was not corroborated in the laboratory studies described herein. While field observations at the peak of early season burial activity in small pads suggest that up to 90% of dung of this type may be removed, seldom during the greenhouse experimentation was a burial level of 50% exceeded. The reason for this discrepancy may be related to the quality of the dung obtained from the dairy. The dairy cattle were fed a supplementary ration of alfalfa hay, so that short tough stalk residues were always present in the dung. These residues may have interfered with collection of dung by beetles during the process of brood ball formation. Beetles evidently sorted the larger alfalfa fragments from the other dung components and left them above

ground. In contrast, the dung of cattle that graze the early season green range grass is probably almost devoid of hard stalk fragments and would be a more homogeneous material for manipulation by beetles.

The small field pads that O. nuchicornis may remove almost completely represent only a fraction of the total dung being passed by cattle in early summer. The beetles do not have any pronounced effect on the more numerous larger pads. In addition, the period of greatest dung burial activity by O. nuchicornis does not coincide with that of maximum horn fly abundance. As beetles may be considered to be out of action from the middle of July through August, while the horn fly at this time is abundant, there is no chance of the beetle exerting any controlling effect, particularly in view of its poor performance with large pads which may yield many horn flies. Table VI showed that non-burying O. nuchicornis, even in comparatively large numbers, normally are not harmful to horn flies. The only exception to this might be during the midsummer dung-shredding period, though not all pads are fully shredded at this time so that there appears to be ample opportunity for some coprophagous flies to breed.

The efficiency of O. nuchicornis as a dung burier does not compare favourably with reports on the activities of two other species. Both are larger beetles capable of colonizing bovine dung pads in numbers sufficient to cause their rapid removal. Bornemissza (1970) found that 30 pairs of the Afro-Asian O. gazella removed an entire 1,000 cm^3 dung pad within 36 hours. When the beetle was introduced into Australia, studies in one release area at the height of beetle activity showed total destruction of cattle dung pads within 48 hours of deposition (CSIRO, 1970).

One of the largest members of the genus, O. quinquedens Bates, buries cattle dung pads in as little as 3-4 hours in the highlands of eastern Africa, throughout an activity season of about six months (CSIRO, 1972). These figures show the high dung removal potential of very efficient tropical species of Onthophagus and may represent an extreme of activity that temperate species are unable to meet on a daily or seasonal basis.

Speed of dung burial by beetles in the field must be a function of the intrinsic burial capacity of a particular species with dung of a certain quality, and of the numbers of this species that normally colonize a given mass of dung in this situation. The first can be determined by insectary experiments; the second, with exotic beetles destined for introduction, cannot be predicted with certainty.

CHAPTER III - NITROGEN IN CATTLE DUNG

INTRODUCTION

Animal feces constitute a rich source of plant nutrients. In natural systems these are returned to the same general area from which they originated. The mere deposition of fresh dung on the soil surface, however, in no way guarantees that its nutrients will be assimilated rapidly into the system. Depending on such factors as temperature, precipitation, and the nature of the dung fauna, the incorporation of dung into soil may range from rapid and almost complete to very slow and incomplete. In the latter case there is a tie-up of the nutrients contained in the dung material.

The major components of cattle dung apart from water are undigested and finely divided plant remains, endogenous secretory and excretory products, bacteria, yeasts, molds and other microorganisms and products of their metabolism, and cellular debris from the gut mucosa (Miller, 1961; Marsh and Campling, 1970; Greenham, 1972). Several workers have published data for some of the major nutrients contained in cattle dung, and the proportion of each nutrient in dung and urine. This partitioning of excretory nutrients by the grazing animal is of great importance in nutrient recycling; in general, those nutrients contained in the urine will be made available to plants much more quickly than those in the feces (Barrow, 1967), where they are held mainly within the organic matter.

Petersen, Woodhouse, and Lucas (1956) estimated that fresh cattle feces in North Carolina contained 0.38% nitrogen (N) on a wet weight basis, while the fresh urine contained 1.10% N, or about three

times as much N as was present in dung. These workers also found that mature cattle produced about three times as much dung per day as they did urine, so that total N excreted daily was about equally divided between feces and urine. The 1:1 ratio of fecal to urine N in this area was confirmed by Lotero, Woodhouse, and Petersen (1966). However, Gillard (1967) in South Africa estimated that up to 80% of excretal N of cattle was present in the feces.

The composition of cattle dung and the partitioning of nutrients between dung and urine will vary under the influence of many factors, among them the season, the forage quality (digestibility), and the age of cattle. It appears that above a certain threshold N level the amount of N present in feces remains fairly constant per unit of dry matter eaten. The average value is about 0.8 g of N per 100 g of dry matter consumed, and the excretal N in excess of this value appears in the urine (Barrow, 1967). Therefore, as the N content of feed increases above the threshold level, the proportion of N in feces decreases. Cattle grazing on low-quality native pasture, as in Gillard's (1967) study, would be expected to have a lower N content in their forage and hence a greater proportion of N in their feces than the cattle of Petersen et al. (1956) and Lotero et al. (1966) that grazed on improved temperate pastures.

Nitrogen in dung is of special interest because it is subject to loss while the dung pad is drying out on the soil surface. Gillard (1967) measured a total N loss of about 80% from dung pads while they dried on pasture in both South Africa and northern Queensland. This is a serious situation in a native pasture that is receiving no artificial fertilization because the dung in such cases contains the major portion of excretal N. Gillard's figure indicates that theoretically up to 64%

of total excretal N could be lost in this way if the system were being grazed very heavily. In the long term this could lead to pasture deterioration from N depletion depending on the actual grazing use.

The amount of N loss determined by Gillard (1967) was not matched in an experiment conducted in New Zealand by MacDiarmid and Watkin (1972). Total N loss after 13 days was only about 11% and the rate of loss had slowed appreciably at this time. No N figures were given for dung which had been totally air-dried under New Zealand conditions. It was evident that N loss is most rapid during the first few days after the dung is voided.

According to Gillard (1967) most of the N present in feces is contained in undigested protein that is utilized by bacteria. Following the reports of Miller (1961) and Mason (1969) it seems likely that much of the N in cattle dung spends some time as a constituent of microbial tissue. Bacteria mineralize some of the organic N to the ammonium form. Ammonia is the typical excretion product of many groups of microorganisms when they are living in N-rich organic matter (Russell, 1961).

The ammonium liberated by bacteria may be immobilized in turn by further incorporation into microbial tissue. Alternatively, it may be lost by volatilization of ammonia (Gillard, 1967). A third possible avenue is utilization by nitrifying bacteria which ultimately convert it to nitrate, but this is probably not an important process in fresh dung.

Insects present in dung may influence ammonia loss. The larvae of muscoid flies are characteristically the most prevalent coprophagous colonists of dung while it is relatively fresh. They utilize the dung when its nutrient content is at a maximum. The maggots develop quickly and tunnel actively through the dung mass. During their

development they influence the physical, chemical, and microbiological nature of the dung in the following fashion:

1) Continuous larval movement churns the dung mass and results in a noticeable increase in its fluidity (Valiela, 1969). This normally results in sufficient moisture being available for larval development in at least the central portion of pads even when there is a thick dry crust present. The repeated churning probably also increases aeration throughout the pad.

2) MacFayden (1964) considered that detritus feeders greatly accelerate the activities of microorganisms in soil organic matter in at least two ways, namely by spreading spores and by breaking down microbial antagonisms. Larval Diptera probably have the same effect in dung, their movements serving to mix and redistribute microorganisms within the dung mass. Furthermore, these larvae are considered to be largely microphagous (Miller, 1961; Dowding, 1967), so that they consume microorganisms and their products continuously while moving through the dung. Feces thus constitute a medium for growing the microorganisms upon which the larval Diptera feed (Baumberger, 1919). Substantial and repeated removal of microbial populations by fly larvae will stimulate their regrowth and tend to maximize their metabolic activity, in the same way as MacFadyen (1961) described for arthropods "browsing" microorganisms in the soil. The resultant microbial heat of fermentation together with the metabolic heat of the larvae should provide favourable conditions for evolution of ammonia gas.

3) The larvae add their own waste products to the dung mass. Brown (1936, 1938) showed that larvae of a sarcophagid and two calliphorid fly species produced the bulk of their excreta as ammonia rather than as

uric acid and that the ammonia appeared in the food residue as ammonium bicarbonate. These sarcophagous larvae primarily ingest protein and its breakdown products, as well as microorganisms, thereby having a diet rich in N that creates special excretory needs. Experiments have shown that house fly larvae also produce ammonia in large amounts, under certain conditions approaching the output of larvae of a calliphorid species (Aksinin, 1929, cited by West, 1951). It thus seems possible that larvae of all coprophagous Diptera feeding in fresh dung may emulate their ammonotelic relatives by also excreting quantities of ammonia into the dung mass. If this occurs, the ammonium bicarbonate may be decomposed by solar heat or microbial action to form gaseous ammonia, thus contributing further to nitrogenous losses from dung. Gillard (in litt.) advised that during his investigations on N loss from dung in the absence of dung-burying beetles, dipterous larvae were observed in some of the pads. These insects were natural colonists and would have removed some N in their bodies when they matured but there is the possibility, especially in view of the 80% loss of N observed (Gillard, 1967), that they may have also promoted additional gaseous losses of N.

Some experiments were conducted during 1972 to assess the actual N loss from dung pads in Kamloops and to establish whether or not coprophagous muscoid larvae are instrumental in increasing this loss beyond the amount of N they remove in their tissues.

MATERIALS AND METHODS

Fresh dung was obtained from the Tranquille School dairy farm and thoroughly mixed. Samples of dung (usually 200 or 250 g) were weighed and then formed into pads as previously described.

Larger pads up to 960 g were made by weighing the requisite amount of dung into a waxed food carton. The dung then was poured out and formed into a round flattened symmetrical pad.

To measure the total N loss and rate of loss from dung pads as they dried out in the sun, ten 250-g dung pads were weighed onto flat light aluminum dishes and placed outdoors in a screened cage to exclude insects. A clear plastic roof above the cage kept precipitation from reaching the dung. Two similar pads were prepared as controls and dried immediately. Pairs of pads were removed from the cage at intervals of 2, 4, 8, 16, and 32 days and oven-dried before N analysis. A similar experiment was performed later to check the original results; the 2-day and 32-day exposures were omitted from this.

A smaller experiment was performed to investigate total N loss and rate of loss from 960-g pads in the absence of insects, because these dry out more slowly than pads weighing 250 g. Hence there may be more opportunity for N loss from the larger pads. Pads were prepared on aluminum dishes containing a little coarse vermiculite and exposed outdoors in a screened cage for periods up to 16 days before being oven-dried for analysis.

All the prevalent muscoid species at Kamloops were considered for use as coprophagous larvae in this work. Adults of these species with the exception of the horn fly are difficult to obtain in the field in numbers necessary to provide a good supply of eggs or larvae. House fly larvae were used instead because they can be obtained easily. A colony of the flies was maintained at Kamloops during 1972.

A small exploratory experiment to investigate the contribution of dipterous larvae to N loss from dung was started in early August 1972.

Single pads of 960 g fresh weight were used with two exposure times (10 and 16 days) and a single level of larval infestation (450 first instar house fly larvae). Two more pads served as controls, one for each time of exposure, while another fresh pad was exposed in a cattle pasture, to give an estimate of actual N losses under conditions of natural colonization by insects in the field. Pads rested on identical quantities of coarse vermiculite in aluminum pans, and all except the pad destined for the cattle pasture were placed in a screened cage before being exposed outdoors. House fly larvae left the dung and pupated within 10 days. At this time the first pair of pads was removed and oven-dried. Also, the original aluminum pan beneath the other (i.e., 16-day exposure) pad containing fly larvae was replaced after 10 days by an identical pan of moist vermiculite, so that the fly puparia could be dried. Puparia were recovered after drying so that they could be weighed and analyzed for N content. No attempt was made to collect fly puparia from the pad exposed in the cattle pasture.

The second experiment of this type used increasing numbers of house fly larvae in a series of similar dung pads. Dung was prepared in six 960-g pads as before and one pad was dried immediately. The other pads had either 0, 100, 200, 400, or 800 freshly hatched house fly larvae added to them, and they were exposed in the outdoor cage for 10 days. After drying, puparia were recovered from the vermiculite and weighed.

Pads in early experiments were dried at 100°C. It then became apparent that this temperature might be causing extra N losses. Drying temperatures were reduced to 70°C, which extended the drying time by 3-4 times the original period.

Pads after drying were ground at high speed to pass a 1-mm screen in a large Wiley mill. Each sample was then throughly mixed,

quartered, and a subsample was taken. Total N analysis was performed mainly on a Perkin-Elmer Model 240 elemental analyzer located at Simon Fraser University. Exploratory experiments were conducted during 1972 at Kamloops and for this work, especially for analysis of fresh dung, the analyzer could not be used. Nitrogen analysis at Kamloops was therefore performed by a micro-Kjeldahl method (Perrin, 1953). The difficulty of weighing fresh dung and manipulating it into Kjeldahl digestion flasks was overcome by the use of small specially constructed hollow glass bubbles.

The elemental analyzer is normally very accurate but in practice its precision is limited by the quality of the sample used. In the current work, every reasonable effort was made to obtain homogeneous ground dung samples. However, because the analyzer used 3 mg samples as opposed to 50 mg samples for the Kjeldahl method, the latter was considered to offer better estimates of total N in the dung.

Many dung samples were analyzed by both the micro-Kjeldahl method and also by the elemental analyzer during the course of this work. The analyzer results were used as a standard to assess the recovery of N by the Kjeldahl method.

Acetanilide was used for standardizing the analyzer and it normally showed greater than 99% recovery of N. The Kjeldahl method gave a recovery of 86.7% N for pure acetanilide (mean of 10 samples). It recovered 86.0% of N in dung samples as compared with that recovered by the analyzer (mean of 29 samples). The latter recovery figure was used to construct a correction factor (1.163), which, when multiplied by the observed per cent N determined by the micro-Kjeldahl method, gave an estimate of the absolute N percentage.

The reason for the consistently lower values obtained by the micro-Kjeldahl method is not known. The general method used was designed for the determination of reduced N as found in most biological samples, and normally gives a good recovery of the element from refractory materials (Hiller, Plazin, and van Slyke, 1948; Lake, McCutchan, van Meter, and Neel, 1951; Perrin, 1953).

RESULTS

Loss of Dung Nitrogen During Oven-Drying.

Four separate determinations were made of N loss from fresh dung when it was dried at various temperatures. All figures were obtained by Kjeldahl analysis. The results are shown in Appendix IV.

In all cases the dung lost N, in one case up to 10.1% of the total fresh N. The loss is large enough to warrant recognition in certain experimental work. In spite of early indications, no evidence was found that drying dung at 50°C, 70°C or 100°C caused differing N losses.

Nitrogen Loss from Dung Dried Naturally.

The first indication of amount of N loss from dung exposed to natural drying conditions suggested that little occurred. In an experiment not directly related to this subject, three 200-g pads were exposed to sunlight on damp soil in a greenhouse for six days and three similar pads were dried immediately for subsequent moisture determination. Nitrogen analysis on the dried pads gave the following results (mean %N and range):

Dung dried immediately: 2.45 (2.34-2.52)

Dung exposed for 6 days: 2.62 (2.45-2.86)

There is no significant difference between these means. Taking into

account the loss of N that occurs during oven-drying of fresh dung, no greater loss was incurred in leaving pads to incubate in warm temperatures for six days.

When 250-g pads were exposed outdoors for various periods, no loss of total N was observed. Instead, as the time of exposure increased the per cent total N rose in both experiments (Table VII). Regression analysis showed that there was a highly significant relationship between the time of exposure before oven-drying and observed per cent N for the first 16 days in the May experiment ($N=10$; $Y=2.33 + 0.02X$; $r=0.941$; $P<0.001$). Dung moisture figures showed that within 16 days the pads had become air-dry. After this time they can be considered relatively inert insofar as N transformations are concerned. A significant regression was also present in the August experiment ($P<0.01$).

In the May experiment, dung contained 10.5% more N after being exposed for 16 days before oven-drying than it contained after being oven-dried when fresh.

Table VIII shows the N content of 960-g pads after various periods of outdoor exposure. A trend of increase in mean per cent N is evident with length of exposure before oven-drying, after the fashion of that observed in Table VII. Even in these larger dung pads no loss of N was demonstrated with increasing time of outdoor exposure.

Nitrogen Loss from Dung Infested with Muscoid Fly Larvae.

Results of the first exploratory experiment that utilized house fly larvae are given in Table IX. Pads in treatments that contained house fly larvae appeared to have lower N contents than treatments exposed for the same time but without larvae. The amount of N recovered in puparia

Table VII Nitrogen and moisture contents of 250-g dung pads exposed outdoors for different times on two occasions in 1972.

Exposure	Mean per cent N[a] May[b]	Mean per cent N[a] August[c]	Per cent moisture May	Per cent moisture August
Nil: oven-dried immediately	2.34	2.07	86.4	86.2
2 days	2.35	---	76.1	---
4 days	2.37	2.05	57.1	48.0
8 days	2.52	2.15	38.1	31.4
16 days	2.62	2.19	13.8	13.9
32 days	2.55	---	13.8	---

[a] Dry weight basis.

[b] Means of micro-Kjeldahl determinations on samples from duplicate pads.

[c] Means of analyzer determinations on samples from duplicate pads.

Table VIII Nitrogen content of 960-g dung pads exposed outdoors for various periods in the absence of other insects.

Exposure	Mean per cent N[a,b]	Range
Nil: Fresh dung (analyzed immediately)	2.23	2.13 - 2.34
Nil: oven-dried immediately	2.11	2.08 - 2.14
4 days	2.12	2.08 - 2.16
10 days	2.14	---
16 days	2.19	2.17 - 2.20

[a] Dry weight basis

[b] Means of duplicate determinations on samples from single pads, except for the fresh dung (6 determinations).

Table IX Nitrogen content of 960-g dung pads that were exposed outdoors for 10 or 16 days. Two of the pads were each infested with 450 house fly larvae and another was exposed to normal colonization by dung insects in the cattle pasture.

Treatment	mg N per pad[a]	mg N recovered in puparia[b]	mg N loss not accounted for	Total loss as % of fresh N[c] content
Exposed 10 days, no larvae	2773.4	---	---	4.0
Exposed 10 days, 450 larvae	2643.8	104.9[d]	24.7	8.5
Exposed 16 days, no larvae	2838.2	---	---	1.8
Exposed 16 days, 450 larvae	2669.8	107.8[e]	60.6	7.6
Exposed 16 days in cattle pasture	2501.3	---	---	13.5

[a] Means of duplicate determinations on samples from single pads

[b] 11.09% N

[c] The fresh dung contained 2890.1 mg N per pad

[d] 220 puparia recovered; dry weight 946.1 mg

[e] 339 puparia recovered; dry weight 972.4 mg

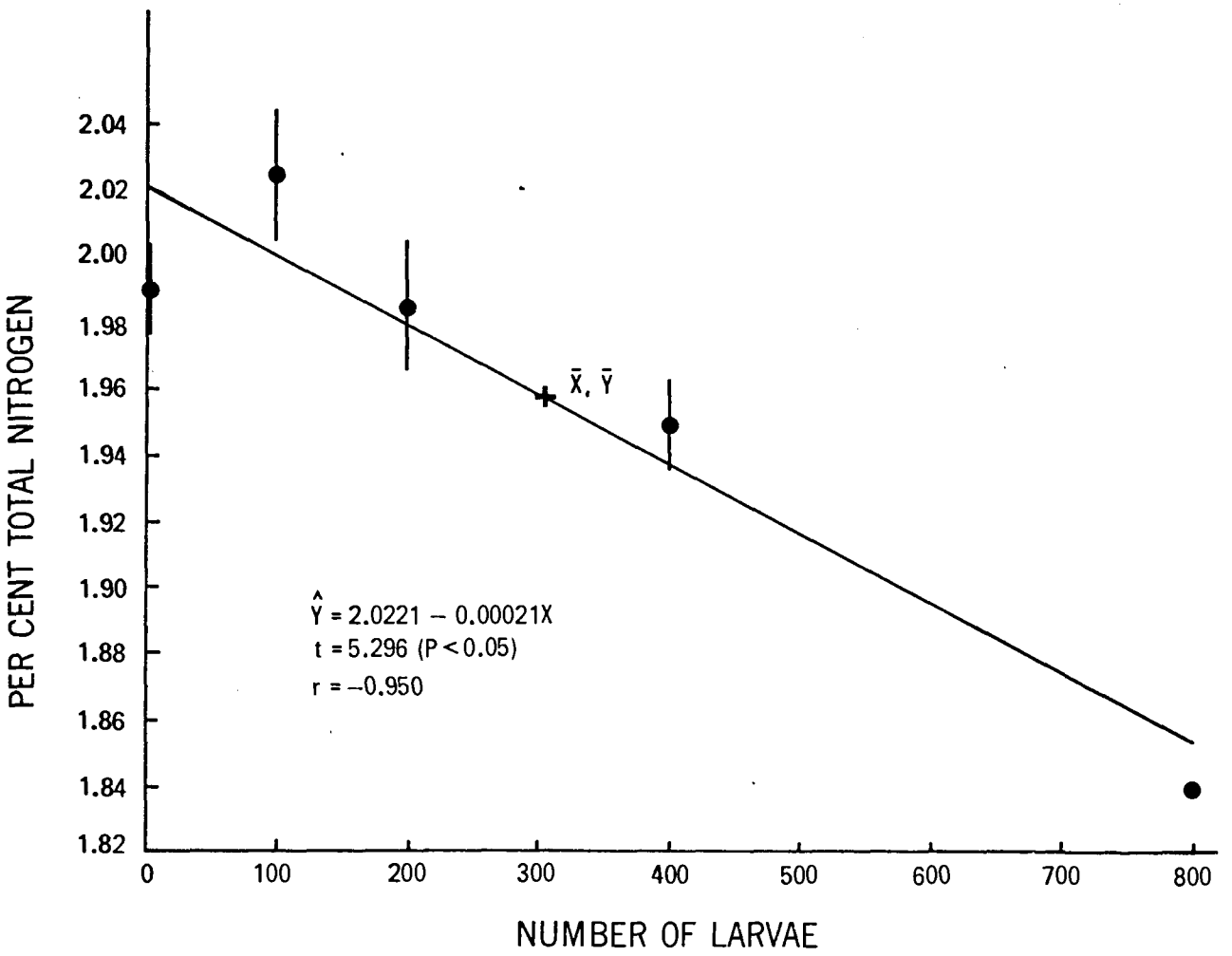
from the two infested pads was similar. However, there was some N loss that could not be accounted for in terms of insect biomass, and this seemed to be greater in the pad that was exposed for 16 days. This is almost certainly caused by difference in time of exposure before drying. The 10-day pads gave lower readings for unaccountable N loss than the 16-day pads, because the 10-day control pad can be expected to have a lower N content after drying than the 16-day control pad. Apparent total N loss from pads infested with fly larvae was similar. Greatest loss of N was indicated in the pad that was exposed to other insects in the cattle pasture.

When 960-g dung pads were colonized by different numbers of house fly larvae during 10 days in an outdoor cage, their N content after oven-drying bore an inverse relationship to the original number of larvae used (Fig. 23). Calculations showed that only in the pad that contained 800 larvae was there an appreciable loss that could not be accounted for by N removed in insect tissue. Here, the puparia contained 42% of the missing N, and the balance (58%) was lost directly or indirectly as a result of larval activity. Thus high numbers of muscoid larvae appear to promote loss of more N than they actually remove from dung in their tissues.

DISCUSSION

Some N is lost from freshly passed dung when it is subjected to 50°C or more for an extended period (Appendix IV). For a given sample of fresh dung, lowest N values were measured on portions that were dried immediately. Table VII showed that the N content then increased relative to these values as the interval between dung deposition and oven-drying

Figure 23 Regression of final percent total N content of 960-g dung pads on the number of house fly larvae that developed in them. Values given are the means ± SD of duplicate N determinations on samples from single pads.


PER CENT TOTAL NITROGEN
2.04
2.02
2.00
1.98
1.96
1.94
1.92
1.90
1.88
1.86
1.84
1.82
0
100
200
300
400
500
600
700
800
NUMBER OF LARVAE
X̄, Ȳ
Ŷ = 2.0221 – 0.00021X
t = 5.296 (P < 0.05)
r = –0.950

was extended. There is no question here of an absolute increase in dung N content after it is voided; in no case did the maximum N content of dung that was left undried for various periods exceed that determined for the same dung while fresh and undried.

It seems probable that in fresh dung used in this study, up to about 10% of the N was present in the form of heat-labile compounds. If fresh dung is dried immediately all this N is lost. If left in the moist state, action of microorganisms or other processes may "fix" the labile compounds progressively, so that little remains to be volatilized when the pad is approaching the air-dry state. Table VII (May) reveals that N content of the dung dried immediately was about 90% of that dried at 16 days. As up to 10% N may be lost by oven-drying while it is fresh, the value obtained for the dung dried after standing for 16 days probably approximates the original N content of this dung before it was dried.

These figures also suggest that the undisturbed 250-g pads actually lost very little N while they air-dried. With larger pads (960 g, Table VIII) the evidence is the same. Even with insects present in the pads, heavy use by coprophagous larvae (i.e., house fly) caused a loss of up to only 8.5% N while loss after 16 days in a cattle pasture amounted to 13.5% (Table IX). These losses were quite small, but must serve only as an indication because they were measured under rather restricted conditions. The extra losses caused by insects may be due mainly to ammonia excretion by fly larvae and its subsequent volatilization, while better aeration due to larval activity might encourage more microbial action leading to increased N conversion and release.

It can be assumed that the major N loss occurs during the first couple of weeks after deposition when rapid changes in moisture

and microbial content are occurring in pads. MacDiarmid and Watkin (1972) demonstrated a loss of about 11% N (5% as ammonia) from dung pads over 13 days in New Zealand. Included in this loss would have been some drainage of dung fluids into the soil, thereby removing some dissolved and particulate organic matter from the pads. Therefore the measured N loss from dung pads does not necessarily represent total loss to the system.

The result of Gillard (1967), who observed an 80% loss of N from dung pads while they air-dry, has thus not been confirmed either in the present experiments, or by MacDiarmid and Watkin (1972). Gillard's work was done in the tropics and subtropics where mean diurnal temperatures are uniformly higher than those of temperate regions. Maximum daily temperatures at Kamloops usually ranged from 27°C to 35°C during August 1972, with minima at least 15°C or even 20°C lower. Such daily fluctuations would not allow high temperatures to develop within dung pads. The effect of increased mean daily temperatures on dung in the tropics might independently promote increased gaseous loss of N from pads.

Higher ambient temperatures in warm climates also mean faster developmental times for fly larvae. Larvae that develop completely during the first 3-4 days while the dung still retains much of its moisture may promote faster N loss via their metabolism than larvae whose development is retarded by lower temperatures. When low or moderate mean daily temperatures prevail, as often seems to be the case at Kamloops, muscoid larvae have to complete their development in dung from 6-8 days old, which may have lost a considerable proportion of its original moisture. Here the churning action of the larvae helps to maintain sufficient moisture for their development (Valiela, 1969) but lower temperatures may reduce microbial activity and the tendency for nitrogenous products to volatilize.

The major microbiological transformations of N occurring in dung apparently have not been investigated in any detail.

Quality of the dung also will likely affect the amount of N loss. Feces produced by animals grazing on fresh young pastures usually are high in moisture and N with low fibre and hence low organic carbon content. This is probably a more favourable substrate for microbial growth leading to volatilization of ammonia than dung from cattle grazing mature pastures that are low in N and much higher in fibre. The investigations described herein always used dung from the Tranquille School dairy where an alfalfa supplement was fed to the cattle. Alfalfa helped to stabilize the consistency of the dung throughout the summer, but in so doing may have masked natural variations in dung N loss as pasture quality fluctuated. Hence there is no guarantee that N loss in range and pasture parallels that observed for the dung from the dairy. As the number of bacteria per gram of dung has been shown to vary considerably between individual cows and between diets (Percival, 1910), the amount of N that is lost by cattle dung may vary greatly even under constant experimental conditions.

Assuming that N loss occurring in dung dropped in rangeland is of the same low order as that observed for the dairy cattle dung in this study, there is still a problem involving the lack of an efficient recirculation mechanism. The total quantities of nutrients returned by cattle to the native range are small. For example, the upper grassland in good condition at Kamloops has a carrying capacity of 1.1 acres per animal unit month (Tisdale et al., 1954). A single beef animal during the course of one month will then graze and void dung over 1.1 acres, at the rate (Marsh and Campling, 1970) of twelve 4-pound pads per day. Each dung

pad will contain a maximum of 7.5 g N of which at least 10% will be lost through insect uptake, ammonia volatilization, and maybe other avenues. The net credit in terms of organic N might approximate 5 lb/acre per month of use, most of which remains on the surface in discrete piles for prolonged periods. In the lower range, with a grazing capacity of approximately 3 acres per animal unit month (Tisdale et al., 1954), N in dung being returned to the soil would be roughly 1.8 lb/acre for each month of use. In spite of the small quantity of N involved, plants should derive benefit in the long term from its incorporation into the soil by dung beetles.

CHAPTER IV - CATTLE DUNG IN RELATION TO RANGE PLANT GROWTH

INTRODUCTION

The sight of dry undecomposed cattle dung pads in the Kamloops rangeland first suggested to me that the area is deficient in dung-burying insects. The pads are not particularly conspicuous on the open range because they are often hidden by sagebrush or other plants. Moreover, the stocking rate of these native pastures is relatively low (Tisdale et al., 1954), and this causes pads to be well scattered. Dried dung pads are most noticeable around watering places, sites providing mineral licks, and cattle "camps".

There is good reason to believe that the range pastures evolved under relatively light and strictly seasonal grazing pressure from the present indigenous ungulates, which are the mule deer (Odocoileus hemionus hemionus (Rafinesque), and the California bighorn sheep (Ovis canadensis californiana Douglas). Bighorn sheep today occur naturally only in a few scattered groups in the Southern Interior of British Columbia. They apparently once ranged over a much wider area (Cowan, 1940; C.J. Guiget, personal communication).

The deer have probably always grazed in the same manner as they do now where undisturbed, utilizing the forage of the forest areas in summer and fall and that of the grasslands in winter and spring (Tisdale, 1947). Other herbivores in the area include the snowshoe or varying hare (Lepus americanus pallidus Cowan), the pocket gopher (Thomomys talpoides incensus Goldman), the mountain vole (Microtus montanus canescens Bailey), and the yellow-bellied marmot (Marmota flaviventris avara (Bangs)). Many species of

grasshopper are present also (Treherne and Buckell, 1924). While little is known of the numbers of animals that originally existed in this region, it is believed that they were not sufficient to cause overgrazing, except perhaps locally during drought years (Tisdale, 1947).

When domestic cattle were introduced in large numbers to the area after 1860, their grazing pattern was superimposed on that of the native animals. The rangelands thus came under constant heavy grazing pressure from an animal with which they did not evolve, and to which no adjustment could be made quickly. East of the Rocky Mountains, where large herds of native ungulates roamed without interruption from Oligocene time until recently, rangelands recover quite rapidly when given a respite from grazing (Daubenmire, 1970). In contrast, the perennial native grasses in the rangelands of British Columbia are unable to endure heavy grazing, and regeneration time after prolonged misuse may require from one to two generations (McLean and Marchand, 1968; McLean and Tisdale, 1972). This phenomenon at least partly reflects a long history of freedom from grazing pressure (Daubenmire, 1970).

The grasslands bore the brunt of the grazing onslaught until the early 1900's (Tisdale, 1947), by which time reduction in carrying capacity had occurred. Ranchers were then forced into utilization of the forest areas. The major problem of grassland ranges in British Columbia is still poor condition and consequent reduction in carrying capacity (Tisdale et al., 1954; Mason and Miltimore, 1959). While there are currently a few large areas of good grassland in the region, range improvement still has priority as a management objective. The need for methods of increasing the productivity of spring and fall ranges is

critical (Mason and Miltimore, 1969).

The major indicator of range deterioration is a change in botanical composition. The originally dominant and perennial wheatgrass Agropyron spicatum (Pursh) Scribn. and Smith including var. inerme Heller is replaced by less palatable species, often annuals, and the proportion of big sagebrush (Artemisia tridentata Nutt.) and weeds increases (McLean and Marchand, 1968). Considerable soil erosion may occur (Spilsbury and Tisdale, 1944). The decline in condition of the range is particularly serious because the grasslands are limited in extent and are of vital importance for spring, fall, and winter grazing.

Cattle are responsible for this decline, through a complex of activities whose individual contributions to overall deterioration would be hard to define. Foremost amongst these is grazing for prolonged periods in the late spring when wheatgrasses are in a critical stage of their growth. There is a trampling effect, causing increased mechanical damage and weakening, and also a disruption of the original nutrient cycles.

Deer are still present in the area, so it is unlikely that any insects originally associated with their dung have died out. Casual observation of their droppings suggests that insects do not play an important part in the breakdown of the pellets, and rather that these deteriorate very slowly under the influence of weather and the action of microorganisms. This is an indication that in the natural state of this ecosystem, under the presumed relatively light grazing pressure, the immediate return of dung nutrients to the soil was not important in maintaining productivity. At the same time, quantities of plant litter

were produced that probably decomposed fairly rapidly on contact with the soil surface. Total annual turnover of nutrients was relatively small. For example, Power (1972) mentioned that under the natural environment, the quantity of N being cycled annually in temperate grasslands is too small to measure accurately with the research tools available.

The situation has now changed. Often a large proportion of the forage produced annually by the rangelands is consumed by cattle and subsequently converted into bovine feces. Up to 80% may be taken in some cases although the recommended maximum consumption is 55% (A. McLean, personal communication). As a result there is little plant litter left on the soil surface. Originally the litter may have been spread relatively evenly over the range, helping to maintain roughly uniform soil organic matter levels throughout. The dung pads of cattle have now largely replaced the general litter layer, resulting in concentration of undecomposed organic matter in discrete heaps. Moreover, the pads are more numerous in certain areas than in others, indicating some transport of nutrients away from parts of the range. A given area of range soil now apparently receives little organic matter return under the current grazing system until it is covered with a dung pad, when it acquires a heavy dressing of plant remains whose nutrients are released to the system very slowly. The return of organic matter from aerial portions of plants is thus very haphazard.

Ecosystems that have a large residue of nutrients immobilized in organic matter (feces or plant litter) are not as productive as those that are relatively more efficient in the recirculation of nutrients (Gillard, 1967). Turnover of nutrients in an ecosystem may be limited

by the rate of decomposition of organic matter (MacFadyen, 1961). The main apparent limitation to decomposition of dung pads in the semi-arid Interior is that the major portion of each is removed from effective decomposer activity.

The native rangelands in British Columbia are receiving little or no artificial fertilizer. Although native N-fixing legumes are present in the higher grassland and forest range, their numbers are generally low. The productivity of the native pastures therefore now depends largely upon the return of nutrients contained in cattle dung and dead roots, and the efficiency with which decomposition processes release nutrients from these materials for plant use.

It is now known that the rangeland pastures suffer from a general N deficiency. Experiments have been conducted in the grasslands since 1957 to determine the practicability of artificial N fertilization (Mason and Miltimore, 1959, 1964, 1969, 1972; Miltimore, Mason, and Rogers, 1962; Hubbard and Mason, 1967). Results ranged from almost no increase in yield at some sites to more than doubling of yield on others. Crude protein content of wheatgrass was increased (Mason and Miltimore, 1959), as well as its seed production (Miltimore et al., 1962). Fertilization of grass rangelands is not generally recommended because of the complex nature of the response that has been obtained so far. Ranchers are therefore advised to fertilize on a trial basis (Canada Department of Agriculture, 1971) but they make virtually no use of this practice at present (Mason and Miltimore, 1972). Cattle dung is rich in N and other nutrients, and several authors have mentioned the likely beneficial effects on plants of dung buried by beetles (Lindquist, 1933, 1935;

Mohr, 1943; Teichert, 1959; Fincher, Davis, and Stewart, 1971). Gillard (1967) found that active dung beetles in South Africa returned 85-95% of cattle dung N to the soil. More recently, Bornemissza and Williams (1970) demonstrated the beneficial effect of dung burial by beetles on Japanese millet grown in pots.

Since range pasture normally will respond to added N, it should benefit from the activities of efficient dung beetles. The effect of the immediate return of bovine dung on range plant growth has not been assessed. Because Onthophagus nuchicornis is the only common scarabaeine beetle in British Columbia, it was used in 1971 in an experiment to investigate the effects on wheatgrass of incorporation of dung into the soil.

Wheatgrasses originally formed the major component of grassland forage before overgrazing caused their decline. One of the goals of range rehabilitation is to promote their reestablishment and survival. It therefore would be useful to know whether return of dung nutrients by beetles will assist this process.

MATERIALS AND METHODS

Beardless wheatgrass (Agropyron spicatum var. inerme, Whitmar selection) was used in a pot experiment. This palatable grass makes fast growth early in the season, mainly in April, May, and early June in the lower grassland. Seed set occurs before the summer drought becomes acute in this zone and the grass becomes dormant in July and August (Tisdale, 1947). If fall rains are adequate, growth may start again at this time.

At the highest grassland elevations the species may remain green virtually throughout the summer (Tisdale, 1947).

Soil used for the pot experiment was a typical Brown Chernozemic sandy loam from a severely overgrazed portion of range in the lower grassland zone near Tranquille. The organic matter content was 2.3% and pH was 7.3. Available major elements in lb/acre were: P, 50; K, 580; Ca, 4,500; Mg, 1,000+ (determination by courtesy of J. H. Neufeld, Soil Testing Service, BCDA, Kelowna). No analysis was made for nitrate-N, but there is little doubt that the soil was N-deficient (A. L. van Ryswyk, personal communication).

Soil was collected from the surface 15 cm and sieved to pass a 5-mm screen. Pots were made from new three-quart waxed cardboard milk cartons with tops removed. Soil depth in the cartons was approximately 16 cm and the surface area was 196 cm^2. Pots were then placed in a greenhouse and the following treatments were applied, replicated ten times: (1) 200 g fresh dung hand-mixed with soil; (2) 200 g fresh dung plus 5 pairs dung beetles; (3) 200 g fresh dung unburied; (4) Untreated control; (5) 60 lb/acre N as NH_4NO_3; (6) 240 lb/acre N as NH_4NO_3.

Treatment 1 simulated total dung burial by beetles. Onthophagus nuchicornis was used in treatment 2 to bury portion of a dung mass, and the remaining dung was removed after beetle activity ceased. Treatment 3 simulated the current range situation, where dung remains unburied but some dung liquid is soaked up by the soil directly beneath the pad; pads were removed from the soil at the same time as those in treatment 2. Treatment 4 was a control, receiving neither dung nor N dressing. Treatments 5 and 6 were included in particular for comparison

with treatment 1, because they represent respectively "low" and "high" levels of N fertilizer currently being used in restorative range fertilization experiments (Mason and Miltimore, 1969).

It was not possible to have dung analyzed for N before this experiment was established. However, Whitehead (1970), summarizing the estimates of several workers, showed an average range in cattle fecal N content of 2.0-2.8% on a dry weight basis. The lower figure of 2.0% was used to calculate a standard amount of dung to apply to pots in treatment 1, so that each initially would receive at least as much N as did treatment 6 (240 lb/acre). The additional elements in the dung besides N actually made treatment 1 nutritionally superior to treatment 6. In view of the anticipated temporary immobilization of dung nutrients in treatment 1, contrasted with the immediate availability of N in treatment 6, information was desired on the relative rapidity and duration of plant response from both these treatments.

The dung treatments were applied in early May 1971. Two days prior to this, water was added carefully to all pots except those in treatment 1, which were kept dry to facilitate uniform mixing of soil with dung. During the watering the N was added to treatments 5 and 6. Firstly 300 ml of water were applied to each pot, thus establishing a wetting front in the soil. The required amount of ammonium nitrate was applied in 100 ml of solution to each pot, followed by more water.

Fresh dung was obtained from the Tranquille School dairy and thoroughly mixed. Samples of 200 g were prepared in the normal manner. In treatment 1, the soil in each pot was thoroughly mixed with 200 g of dung and then water was added.

Onthophagus nuchicornis beetles were collected from cattle pastures for use in treatment 2, and handled as previously described. Five pairs were placed in each pot of treatment 2 after the dung pad had been added. These pots were covered with fine mesh nylon screen. Similar dung pads were placed in each pot in treatment 3.

Beetles were kept in the pots for about 130 hours. Then the remains of the dung pads in treatment 2 were collected together with as much of the shredded dung material on the surface as could be salvaged, and retained after oven-drying for an estimation of per cent burial by the ashing method (see Chapter II, Materials and Methods). Another index of burial activity was obtained by a count of dung balls in the root masses at final harvest in August 1972.

Pads in treatment 3 (unburied dung) were removed from the soil at the same time as those in treatment 2, and were dried and retained for estimations of N, loss of dry matter on standing, and loss of weight on ashing. Dung in treatments 2 and 3 had become noticeably hardened at this stage; pads in treatment 3 at time of removal (130 hours' exposure) had lost about 100 g of water.

The surface soil of all pots was scarified and each was planted with four wheatgrass seedlings. The pots were watered up to the approximate field capacity of the soil (32% moisture - determination by courtesy of D. S. Stevenson, CDA Research Station, Summerland). The experiment was arranged on benches in a greenhouse that had ventilation but no temperature control and that afforded continuous and uniform exposure to sunlight. Pot positions were fully randomized. Several dead or very weak grass seedlings were replaced and the grass was clipped three times in the first weeks to encourage tillering. Water was

added about twice per week, depending on weather conditions.

At the end of August 1971 the pots were finally wet up to constant weight and were then left without additional water for a month. The first harvest was completed at the end of September.

The grass at this stage was well grown and had cured to a large extent. The number of culms and spikes was counted at harvest, then the culms were clipped 5 cm above the soil surface. They were allowed to air-dry, then oven-dry at 100°C. Yields were taken and the plant material from each pot was ground for N analysis and thoroughly mixed to ensure the homogeneity of samples.

The experiment was located in the greenhouse during the first season to promote maximum grass growth and survival. After successful establishment, information was required on the effect of each treatment on the ability of the grass to overwinter. After the 1971 harvest the pots were taken outdoors and moistened almost to field capacity. The experiment was housed during the 1971-1972 winter in a shallow rectangular wooden frame situated in a sheltered position at the Research Station. The aim was to provide some protection from extreme cold while at the same time allowing exposure to snow, ice, and freezing conditions.

In early May 1972, the pots were removed from the shelter and installed outdoors, where they remained all summer. Winter kill of plants was recorded. Spikes were harvested when nearly all were mature on 28 June.

The final harvest was made in late August 1972. Counts were made of the number of culms and also the new fall shoots growing from the base of each plant. Spike lengths were measured and the number of

spikelets was counted. Grass plants were cut at ground level and processed as before for yield and N determinations. Soil was then washed from the roots. Remains of beetle brood balls in treatment 2 were not damaged by the washing process and these were recovered. Roots were oven-dried and weighed. Total yield of tops included the weight of dry matter obtained in the August harvest and the weight of spikes obtained from each pot earlier in the season.

Total N determinations were made on the elemental analyzer, and the crude protein content of the grass was calculated as (% total N) x 6.25. An analysis of variance was performed on the plant production data obtained during both harvests, using the logarithmic transformation where necessary to equalize treatment variances. Treatment means were compared using Tukey's method of multiple comparisons (Scheffe, 1959).

RESULTS

No chemical analysis was performed on the fresh undried dung (86.4% moisture) at the start of the experiment. The dung after oven-drying contained 2.45% N. Taking into account the mean N loss during oven-drying of approximately 8.3% (Appendix IV), this would make the N content of the fresh dung roughly 2.67%.

Pots in treatment 1, where dung was fully buried, thus received dung N at the rate of 330 lb/acre. Dung burial by O. nuchicornis in treatment 2 averaged 27.5 brood balls, representing 37.4% of the pad placed in each pot. The result of beetle activity was an incorporation into the soil of 120 lb/acre of N. An unknown proportion of this was used by the developing O. nuchicornis larvae, because they consumed

varying amounts of the dung food material provided by the parent beetle.

1971 harvest.

The total crude protein content of a quantity of forage (yield x % crude protein/100) is a direct measure of its ability to nourish grazing animals and therefore it provided the most useful basis for evaluating forage production in this experiment.

Total crude protein produced in the wheatgrass tops (excluding spikes) during 1971 is shown in Table X. All treatments except 3 (unburied dung) produced significantly more crude protein than the control. Treatment 2 (beetle-buried dung) produced 40% more, treatment 1 (hand-buried dung) over 100% more, while with fertilizer N, increases over production in the control of 260% (treatment 5) and 320% (treatment 6) occurred. Plants in treatment 6 (240 lb/acre N) gave a higher yield and also had a higher total N content than those in treatment 1 (330 lb/acre N); treatment 1 was superior to the control in both these variables. Treatment 2 (120 lb/acre N) had a higher yield than the control but its total N content was not significantly higher.

There was little difference in the mean numbers of culms produced per plant (Table XI). The fertilizer treatments tended to be most successful in producing spikes, although in this first season of growth very little seeding occurred, and then only in late summer.

1972 harvest.

Eighteen grass plants (out of 240) died during the 1971-1972 winter (Table XI). In addition, eleven other plants overwintered poorly and did not grow vigorously during 1972. Grass mortality was highest in

Table X Effect of cattle dung and N fertilizer on total yield of tops (including spikes) and roots, and % total N and crude protein (CP) content of tops (excluding spikes), of the beardless wheatgrass harvested in 1971 and 1972. Figures given are means of 10 replicates.

Treatment*	Yield of tops (g) 1971	Yield of tops (g) 1972	Yield of roots (g) ** 1972	Root/shoot ratio 1972	% total N in tops 1971	% total N in tops 1972	Total CP in tops (mg)+ 1971	Total CP in tops (mg)+ 1972
DUNG:								
1. Hand-buried (330 lb/acre N)	2.733 c	6.626 b	11.100 b	1.68	2.11 c	0.67 c	361 c	256 d
2. Beetle-buried # (120 lb/acre N)	2.407 bc	5.026 a	8.885 ab	1.77	1.54 ab	0.65 c	235 b	191 bc
3. Unburied	2.097 ab	4.784 a	8.898 ab	1.86	1.60 b	0.55 ab	210 ab	151 a
4. CONTROL	2.005 a	4.984 a	8.576 ab	1.72	1.31 a	0.50 a	164 a	144 a
FERTILIZER:								
5. 60 lb/acre N	2.965 cd	4.999 a	7.292 a	1.46	2.30 cd	0.61 bc	425 cd	176 ab
6. 240 lb/acre N	3.137 d	6.970 b	10.827 ab	1.55	2.66 d	0.60 bc	519 d	234 cd

* Means sharing the same letter are not significantly different at the 5% level.

** Measured at the end of the experiment in 1972.

\+ Means for each treatment differ between 1971 and 1972 (P at least <0.05; t-test).

\# Mean per cent dung burial was 37.4.

Table XI Effect of cattle dung and N fertilizer on production of culms, spikes, spikelets and new fall shoots of beardless wheatgrass in 1971 and 1972. The amount of winter mortality between the two growing seasons is also shown. Figures given are means of 10 replicates.

Treatment*	Culms/plant 1971	Culms/plant 1972	Spikes/plant 1971	Spikes/plant 1972	Spikelets /spike 1972	Spikelets /plant 1972	Spike length (cm) 1972	New fall shoots /plant 1972	Mortality (plants /pot) 1972
DUNG:									
1. Hand-buried (330 lb/acre N)	10.3 ab	10.1 c	0.3 abc	5.6 b	5.2 a	29.9 c	7.4 ab	9.1 b	0.7 c
2. Beetle-buried** (120 lb/acre N)	10.3 ab	9.3 bc	0.0 a	3.5 a	4.3 a	15.2 a	6.8 a	5.5 ab	0.2 b
3. Unburied	9.3 ab	8.4 abc	0.1 ab	3.2 a	4.5 a	14.1 a	7.0 ab	2.7 a	0.0 a
4. CONTROL	8.7 a	7.8 ab	0.2 abc	3.8 a	4.4 a	16.4 ab	6.8 a	2.6 a	0.0 a
FERTILIZER:									
5. 60 lb/acre N	10.9 ab	7.1 a	0.6 bc	4.0 ab	4.4 a	17.3 abc	7.3 ab	3.4 a	0.3 b
6. 240 lb/acre N	11.0 b	9.1 abc	0.7 c	4.4 ab	5.6 a	24.6 bc	8.5 b	6.1 ab	0.6 c

* Means sharing the same letter are not significantly different at the 5% level.

** Mean per cent burial was 37.4.

the treatments that received the heaviest dressings of additional nutrients. Greatest mortality in any pot was 2 plants. Most (40%) of the plants that overwintered poorly were in treatment 6. No allowance was made for the dead or weakened plants when analyzing the results for yield and protein production per pot.

Yield in 1972 was more than twice that of 1971 in most treatments (Table X). Treatment 6 (240 lb/acre N) outyielded treatment 1 (dung: 330 lb/acre N) in 1971 but not in 1972. Yield of treatment 5 (60 lb/acre N) lay between that of treatments 1 and 6 in 1971, but was significantly lower than either of these in 1972.

Total N content of the grass for all treatments in 1972 was roughly one-third of that measured in 1971 (Table X). In addition, the range of N contents between treatments was much reduced. Per cent N in treatment 6 in 1971 was double that of the control, but in 1972 was only 20% greater.

Total crude protein was lower in 1972 than in 1971 for all treatments (Table X). Treatment 1 produced less crude protein than treatment 6 in 1971 but in the following year there was no difference between them in the amount of protein produced. Protein production in treatment 2 was less than that in treatment 5 in 1971. There was no measurable difference in their protein production during 1972.

Fertilizer N at 240 lb/acre (treatment 6) caused the production of the greatest amount of crude protein over two seasons (Table XII). Dung (330 lb/acre N) and fertilizer at 60 lb/acre N induced approximately equal increases in protein production.

Table XII Ranked overall crude protein production in tops (excluding spikes), and corresponding recovery of both dung and fertilizer N by beardless wheatgrass. Totals for 1971 and 1972 are combined.

	Treatment	Crude protein		Total N
		Mean production in tops (mg)*	% increase over control	% recovered of amount added to soil
6.	240 lb/acre N	753 d	144	14
1.	Dung: hand-buried (330 lb/acre N)	617 c	100	7
5.	60 lb/acre N	601 c	95	36
2.	Dung: beetle-buried (120 lb/acre N)	426 b	38	7
3.	Dung: unburied	361 ab	17	?
4.	Control	308 a	--	--

* Treatments sharing the same letter are not significantly different at the 5% level.

Variation occurred in the proportion of dung or fertilizer N recovered in tops (excluding that in spikes) (Table XII). Recovery (treatment N - control N) appeared to be higher for fertilizer N than for dung N during the period of the experiment. The most efficient use of added fertilizer N occurred in treatment 5. Recovery of N from buried dung was uniformly low but in view of the slow release of organic N that is known to occur, this may continue for several years. The recovery figures show that the bulk of the applied N was still in the soil when the 1972 harvest took place. Some more N was removed in spikes, particularly in 1972, but this was not measured. Mean spike weight per pot in all treatments represented a relatively constant 7-9% of total top weight in 1972 [range 0.317 g (treatment 3) to 0.580 g (treatment 1)]. The N in spikes probably constituted a relatively low proportion of the total N removed. Much of the fertilizer N may have become immobilized below ground in the same fashion as has been described by Power (1970, 1972) for another semi-arid grassland soil.

Even if mortality had not occurred in some treatments, it is unlikely that their mean crude protein production per pot would have been higher. When protein production was calculated on a per plant basis, instead of per pot, the same relative performance between treatments was noted as appears in Table X. This indicates that compensatory growth was made by survivors in the pots that lost plants.

When crude protein production for each year was plotted against the amount of fertilizer N added (i.e., for control, 60 lb/acre and 240 lb/acre), the response curve was approximately parallel to the abscissa at 240 lb/acre N. This suggested that 240 lb/acre N may have been about

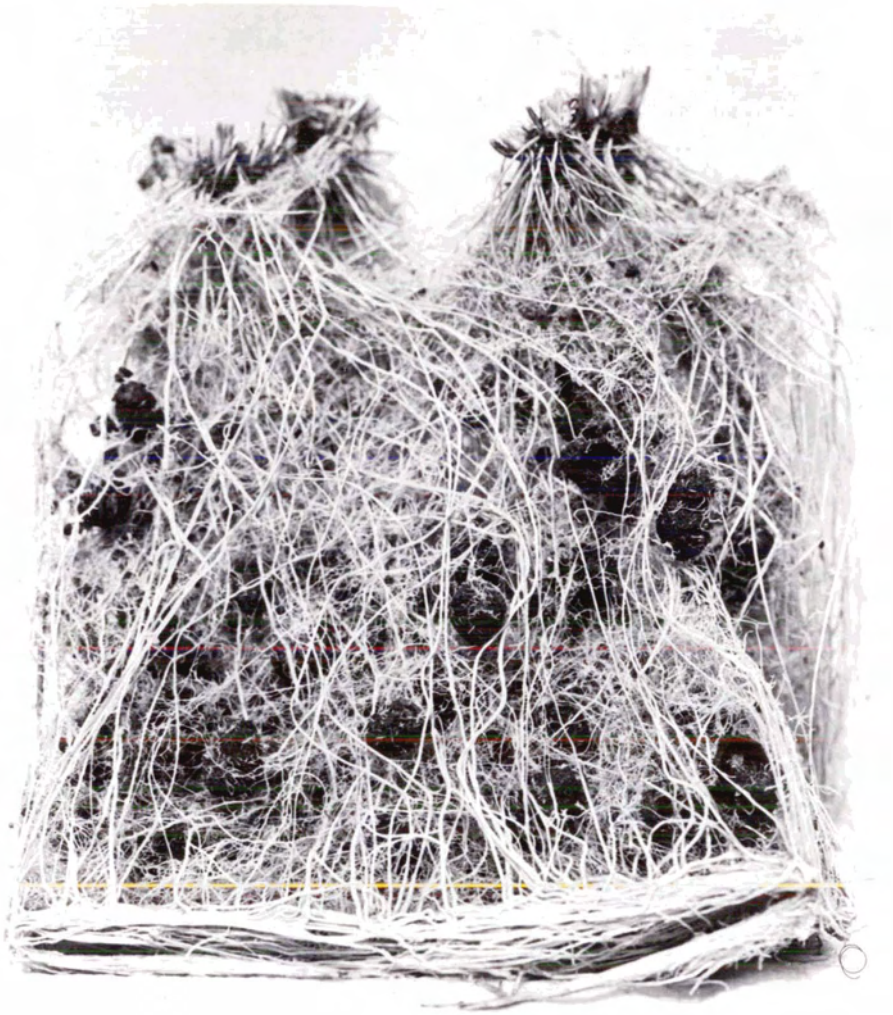
optimal for the conditions of this experiment.

A greater yield of roots was measured in treatment 1 than in treatment 6 during 1972, but no other differences were detected. Because wheatgrasses normally produce a very extensive root system, any treatment which promotes root growth is likely to ensure satisfactory establishment of the grass plants. Root/shoot ratios were apparently lowest in the two N fertilizer treatments, indicating that top growth was encouraged by mineral N at the expense of the rooting system. The arrangement of beetle brood balls amongst the root mass of grass from a pot in treatment 2 is shown in Fig. 24. Each ball was penetrated by a large number of hair roots.

The mean number of spikes produced per plant was much higher for all treatments in the second season (Table XI). The amount of viable seed produced by each plant was not determined, owing to lack of time. Instead, the mean number of spikelets produced per plant was used to indicate potential seed production. Treatment 1 produced significantly more spikelets per plant, and hence potentially more seed, than did treatments 2, 3, or 4. There was an indication that the increase in potential seed production (= spikelets per plant) of treatment 1 was due primarily to an increase in the number of spikes per plant rather than to an increase in spikelets per spike.

From early August onwards in 1972, new fall shoots commenced to grow from the bases of many grass plants. These were used as an indication of relative vigor between treatments. Those treatments receiving the most additional N also produced the greatest number of new fall shoots.

Figure 24 Root mass of beardless wheatgrass containing the remains of brood balls that were made by Onthophagus nuchicornis before the grass was planted.



DISCUSSION

In this experiment beardless wheatgrass showed increases in yield and crude protein production when cattle dung was incorporated into the soil. Potential seed production and apparent vigor of the grass plants also increased in the second year of growth. Greatest response was obtained when small dung pads providing 330 lb/acre N were fully mixed with the soil by hand, representing complete burial of the dung by efficient coprophagous beetles. When dung beetles buried slightly more than one third of the same quantity of dung, crude protein production of the grass also was consistently higher than that of the control treatment. Plants derived little benefit, and then only during the first growing season, from the absorption of fresh dung fluid by soil (treatment 3).

Dung burial compared very favourably with the two levels of N fertilizer in its beneficial effect on wheatgrass. Mineral N, being readily available, provided stimulus for a flush of growth in the first year, which was sharply reduced in the second season. Response to dung was more consistent. The dung and fertilizer treatments are not directly comparable in terms of total added nutrients. Dung is rich in N, and also contains considerable amounts of P and Ca but is low in K (Hutton, Jury, and Davies, 1967). Soil used in the experiment was adequately supplied with P to the extent that Hubbard and Mason (1967) failed to obtain a response to P fertilizer in the lower grassland. Because there is also abundant Ca in the soil (see analysis - Materials and Methods), the primary response of the grass in the dung treatments probably was to the N in the feces. The amount of N initially incorporated into the soil in treatments 1 and 2 is known, but in

treatment 2 an unknown proportion of the 120 lb/acre N was used by O. nuchicornis larvae for their development. Petersen et al. (1956) estimated that cattle dung supplied the equivalent of 760 lb/acre N to the area actually covered by pads in North Carolina. The localized N return to such an area would be considerable if efficient dung beetles were present.

Treatment 1 did not fully duplicate the action of beetles. Beetles bury dung in discrete portions instead of mixing it uniformly with the soil, and in addition, most of the dung buried as brood balls subsequently passes through the digestive tract of the larvae before other soil decomposers have a chance to act upon it. Some of the nutrients in each brood ball are removed by the developing larvae and plants are thereby deprived of them. The progeny leave behind all their fecal material when they emerge from the ball as adults, and this organic matter is rendered more homogeneous in passing through the larval digestive tract. Dung beetles as used in treatment 2 could thus be expected to accelerate the release of available N and other nutrients from dung. The direct return of organic matter will be beneficial not only because of the nutrients it supplies; soil physical characteristics (e.g., structure and water-holding capacity) will also be maintained or improved by such additions.

It might be hazardous to extrapolate the results of this experiment directly to the rangeland. The grass was grown under conditions of good soil moisture, and information is required from field and pot trials where greater moisture stress exists. Lower and middle grassland zones have adequate soil moisture only up to early summer, when the seasonal drought commences and presumably most microbial activity in

soil ceases. Nothing is known of the rate at which dung might decompose in range soil, or the extent to which its N might become available in the field situation. Restrictions imposed by growing the grass in pots may have caused results that are not directly representative of the field situation (e.g., the apparently lower values for root/shoot ratio in the fertilizer treatments).

The mortality that occurred principally in those treatments with the highest N dressings may be an artefact of the experimental conditions, but also might be taken as an indication that the effects of range fertilization and dung burial on grass survival require field investigation. In each pot, four grass plants that normally produce extensive root systems were crowded together, so that induced competition must have been intense. It is not known if the observed mortality has serious practical implications for the field. Nitrogen fertilization, particularly at the high levels which would be essential to produce a response lasting several years from a single application (Miltimore and Mason, 1972), may cause some grass mortality. The added N, by promoting additional growth in the fall, may affect the ability of grass to "harden off" normally before winter, thus increasing its vulnerability to cold.

None of the reports of range fertilization work conducted in the Interior of British Columbia has considered nutrient recycling in this grazing ecosystem. In South Africa, Davidson (1964) showed in fertilizer experiments that N derived from cattle dung that was returned to the soil by dung beetles made a major contribution to the maintenance of pasture productivity. Proper interpretation of his results would have been impossible without a consideration of the nutrient recycling occurring at the same time. Although Davidson stressed that his results

might have limited applicability, they are probably valid for most areas that have an active dung-burying fauna and that in addition are intensively grazed. They also serve to underline a basic deficiency in systems lacking this fauna.

In British Columbia at present, there is a bottle-neck in all plant nutrient cycles that is caused by the slow decomposition of dung pads on the soil surface. Acceleration of the rate of dung decomposition will occur only if feces are incorporated into the soil. In the rangeland, there might be further limitations to rapid liberation of available nutrients from dung after it is buried (e.g., seasonal periods of microbial inactivity due to drought or cold).

In the absence of faster dung removal into the soil, and assuming that the current grazing pressure is maintained, the addition of N fertilizer cannot promote a long-term increase in productivity of depleted range. Range fertilization would have the opposite effect if the short term yield increases encouraged ranchers to increase their stocking rates, thereby stockpiling more nutrients in dried dung pads.

One possibility that does not appear to have received any serious attention is the utilization of introduced legumes to supply N to range pastures and also animals. Pastoral agriculture in many areas of the world now depends on grass-legume associations. It must be admitted that the semi-arid rangelands of the Interior have a climate that most legumes might find hard to tolerate. There is however an unexplored prospect here for obtaining another useful range component that could provide a suitable and continuous supply of the element that most seriously limits range pasture production. In contrast, repeated range fertilization, even if economical, may not prove to be ecologically acceptable.

Fertilizers may nevertheless constitute a very useful management tool for rehabilitation of impoverished range. Dung beetles, if suitable species can be found, might be used as a self-perpetuating tool to maintain range productivity by helping to recirculate nutrients. Neither agent would be useful unless the amount of grazing by cattle is better coordinated with the recognized needs of the native pastures.

If efficient new beetle species were successful in removing cattle dung from these rangelands, the beneficial effects of their activities might not become apparent for some time because of the well-scattered distribution of dung pads, the inherent lag which occurs before most dung nutrients become available, and the depleted condition of some areas of range. On well-managed range, and also on irrigated pastures, response of plant growth to dung beetle activity might be measured in the short term. On depleted range, covered with sagebrush and with few vestiges of the original native grass, no likely measurable effect would occur unless management practices were also changed. Rehabilitation of these areas involves exclusion of cattle, thinning of sagebrush, and reseeding to wheatgrass, possibly with the addition of a little artificial fertilizer to promote establishment and growth of new grass seedlings. Grazing pressure must be reduced after establishment.

The climate in the Interior would undoubtedly preclude any beetle activity before the middle of April (time of cattle release from overwintering paddocks). Little, if any, activity could be expected after early fall when pastures are mature, dung N content is low, and cool weather prevails. The summer drought that is especially pronounced at lower elevations in the Interior could militate against dung burial by beetles that require a certain degree of soil moisture for this activity

(Halffter and Matthews, 1966; Bornemissza, 1969). In properly managed grazing, cattle have in any case left the dry lower range well before the onset of the really dry period. Beetles should follow the herds of cattle as they move higher into the range during the summer. It may be possible to effect dung burial for most of the growing season by carefully monitoring the seasonal activity patterns of candidate beetle species prior to their introduction.

CONCLUDING DISCUSSION

Cattle dung causes persistent problems in rangelands in the Southern Interior of British Columbia. These problems occur to some degree wherever cattle are grazed in the Province. They are most serious in the rangelands in the Interior because these are drier throughout the year and warmer during the growing season than any other provincial region. Consequently the horn fly often is able to build up high infestations due to the favourable temperatures, while the aridity encourages preservation of dung pads rather than their decomposition.

The problems involving breeding of coprophagous flies and immobilization of nutrients that are associated with dung in British Columbia are basically similar to those that occur in Australia, except that here the N loss from fresh dung while it dries does not appear to be as great. The cluttering of grazing lands with dung pads was mentioned briefly in the General Introduction. These pads are also a problem in areas of high carrying capacity that are intensively grazed, e.g., irrigated pastures and dairy cattle pastures in the Fraser Valley and Lower Mainland. In such areas the humidity and precipitation (natural or artificial) causes dung to become fragmented much more quickly than it does in dryland pasture and this often allows pasture grass to grow up through the area originally covered by the dropping although much dung material may still remain on top of the soil. Available nutrients from the dung then produce a flush of growth, which cattle usually tend to avoid unless they are forced to eat it. Norman and Green (1958) suggested that herbage fouled by dung is initially repellent to cattle because of the smell; the herbage, being ungrazed, then becomes mature, coarse and

unpalatable, and later neglect of it by cattle is due to its lowered palatability rather than proximity of dung. An insignificant amount of rank growth normally occurs around pads in areas that receive very little precipitation, such as the lower grassland at Kamloops. Rank growth becomes more noticeable in this rangeland as altitude, and consequently precipitation and available moisture, increase.

Weed growth may be encouraged by dung pads (Bornemissza, 1960), but this aspect was examined only cursorily during the present investigation. Sometimes dung pads in irrigated pastures at Kamloops had more common weeds in their vicinity than were present in the surrounding pasture. In the open range no such effect was noted. Deposition of a dung pad on pasture effectively lowers forage production in the area covered if the feces are not quickly dispersed (Bornemissza, 1960). Some weed seeds, brought in by wind or in the digestive tracts of cattle from other areas, may find these disturbed areas suitable for establishment. Growth of the weed plants might be facilitated by temporary reduction in competition from the grass that has been covered by dung.

The Practical Solution.

Knowledge of the problems involving cattle dung and its associated insects in British Columbia, together with a recognition of the basic reasons for their occurrence, indicates that consideration should be given to introduction of additional dung beetle species into the Province. A beetle introduction program could be justified solely in terms of a desire to reduce the populations of fly pests as much as possible. There is additional justification evident in the other problems that result from the mere presence of undecomposed dung pads on the ground. The original nutrient cycles in the rangelands were altered

when cattle were introduced and allowed to overgraze range pastures without introduction of any of the coprophagous beetles which remove their dung. At present, an outstanding missing ecological component of this grazing system is a beetle fauna that buries cattle dung efficiently.

Halffter and Matthews (1966) recommended the introduction of Scarabaeinae into any areas obviously deficient in buriers of domestic animal dung and provided some basic criteria to be observed when planning such importations. They advised against introductions of dung beetles without thorough preliminary studies, especially studies to determine what influence the introductions may have on the local scarabaeine fauna. To this should be added an extra precaution, namely to determine the possible effect of the local fauna on beetles destined for introduction.

Halffter and Matthews (1966) also noted that most scarabaeine faunas in areas with abundant excrement where both the beetles and the herbivores are indigenous contain several species of diverse habits. Because of this they are seldom in direct competition with one another for dung. Halffter and Matthews recognized that the following forms could coexist naturally in the same area, and moreover, were all needed in a program of deliberate introductions aimed at bringing about the most rapid removal of excrement: one or two species of diurnal large Coprini (the paracoprids of Bornemissza (1969) that construct their nests in the soil beneath or near a dung pad and connected with it by a tunnel during construction); one diurnal species of Scarabaeini (the telecoprids of Bornemissza (1969), known as "tumblebugs" in North America, that make balls of dung from the dropping and roll these some distance away before burying them); plus an equivalent number of nocturnal species belonging to these tribes. They further recommended that these species be supplemented by

two or three species of smaller size, e.g., Onthophagus (paracoprids). An example of natural colonization of cattle dung was provided by Gillard (1967) who gave the following average numbers of true dung beetles of various genera that naturally and typically inhabited cattle dung in South Africa during midsummer: 50 Onthophagus spp.; 50 Oniticellus spp.; 40 Onitis spp.; 2 Copris spp.; less than 1 Heliocopris sp.; 5 Sysiphus sp. The exact numbers of species were not given, but Gillard's table shows that at least nine different paracoprids and one telecoprid (Sysiphus sp.) were present.

It is imperative therefore to investigate thoroughly the diurnal and seasonal activity patterns of prospective beetle species in their native habitat, and then by introduction to make the best combination of species possible on a basis of knowledge of beetle behavior. Introduction of species that have similar habits and activity patterns would be counter-productive because such species would be forced into competition with each other.

Obviously the first task must be to search for efficient Coprini and Scarabaeini to create a major division of labour and so avoid excessive congestion of soil beneath the pad with brood balls and tunnels of the paracoprids alone. It is also preferable from an ecological viewpoint to have dung material from a pad spread over as wide an area as possible instead of being concentrated only in the area covered by the original dropping.

Prospects for Beetle Introductions into British Columbia.

Only a few species of indigenous Scarabaeinae are present in Canada east of the Rocky Mountains. All of these bury some dung but normally not in sufficient quantities to have any useful effect on removal

of dung from pastures (H. F. Howden, personal communication). These beetles were probably associated at one time with the dung of the plains bison which was exterminated in Canada well before the end of the 19th century. When the Canadian Government passed a law conferring total protection on the bison in 1891, the few hundred survivors were wood bison and these lived in a northern wilderness area which is now contained within Wood Buffalo National Park (Banfield and Novakowski, 1960). It is not known if beetles recently played a significant part in removal of plains bison dung in Canada or if any true dung-burying beetles were associated with the northern wood bison. Fragmentary evidence suggests that neither occurred.

At the start of this investigation, it was not known if the dung beetles now resident in southern Canada represented all members of the fauna that were present before the bison disappeared. If other species once existed here, and retreated with the bison, they might still be present in the area which has supported bison without interruption since Europeans colonized North America.

Accordingly, I made a survey of dung beetles associated with bison excrement in Wood Buffalo National Park in August 1970. There are now several thousand bison in the Park. No representatives of the Scarabaeinae were found in this survey and only three species of Aphodiinae were collected.

There does not appear to be any point in looking further in Canada or the northern United States for dung beetle species to introduce into British Columbia. While a survey of the literature reveals that more species of Scarabaeinae are present in the southern part of the United States than in Canada, differences in climate between the two regions

rule out the possibility of using southern species in British Columbia except perhaps those normally living at high altitudes.

A more extensive dung beetle fauna is present in areas of equivalent latitude (approximately 50°) in the Old World. In the Palaearctic Region alone there are several hundred species of Onthophagus, with the range of the genus extending up to about 65° north latitude (Balthasar, 1963b). In this region many other dung beetle genera are found also (Balthasar, 1963a). Only a small proportion of these might find climatic conditions suitable in the Interior of British Columbia. Many genera do not reach 50° north latitude. Hence, with the exception of Onthophagus, which has species with ranges extending well into the cold temperate zones (Halffter and Matthews, 1966), the number of species potentially suitable for colonization in Canada may prove to be quite limited.

If in the future dung-burying beetles are required for introduction, then the Palaerctic Region should be the place to initiate the search for suitable forms, for two reasons:

- areas that are climatically similar to the Southern Interior of British Columbia occur there (Walter and Lieth, 1964, 1967);
- at least one of these areas is known to have indigenous dung-burying beetles that can utilize dung of domestic Bovidae, e.g., the Kirgiz territory of the USSR (Protsenko, 1968), and is within the general area of bovid origin.

No other land mass in the world can provide coprophagous beetles that meet both these conditions, and species may exist there that are capable of colonizing the Southern Interior of British Columbia and

other parts of Canada. However, the suitability of any European beetles would have to be carefully assessed. It cannot be predicted with certainty that there are species in existence which in combination can perform the task efficiently or for the length of time required in the field situation.

The Potential Benefits.

The major benefits that could be derived from a successful dung beetle introduction program in British Columbia have been outlined in each chapter. Some projections can be made about the possible effects of efficient beetles on the three problems that were investigated.

a) Fly pests.

The breeding of horn flies, face flies, and other coprophagous Diptera should be greatly reduced. Initially, reduction in size of dung masses by beetles would concentrate fly larvae and make them more accessible to predators (Bornemissza, 1968). However, dung beetle activity should eventually reduce the numbers of important predators of flies in dung primarily by removing their food supply; these natural enemies depend upon dung to provide the coprophagous fly larvae that form their prey. Onthophagus nuchicornis may suffer competition from introduced beetles and in that case would persist at lower densities. The breeding of Aphodius fossor, A. fimetarius, and smaller Aphodiinae would almost certainly be curtailed, because these species require whole dung masses within which to complete their relatively long periods of larval development. I can forsee no reason why O. nuchicornis or any other components of the existing dung fauna should adversely affect colonization of introduced beetles, but the possibility of this happening should be investigated.

If the new beetles perform satisfactorily throughout the summer then the reduction in entomophagous dung organisms will be of no consequence. In the event that the dung beetles were found to be unable to operate for a certain period (e.g., during the summer drought), horn flies might attain high populations before the end of summer if their predators were unable to multiply sufficiently quickly to provide any significant degree of control. It was shown in this investigation that Sphaeridium species decline in number during August; if introduced dung beetles have previously succeeded in reducing other entomophages (especially Philonthus cruentatus) sufficiently, the horn fly may then breed with little interference. Kunz et al. (1972) showed that the populations of horn fly present in late fall are responsible for the spring buildup of flies on cattle after the winter diapause period. Therefore an increase in horn fly populations in late summer could cause increased annoyance to cattle both at the end of that season and in the early part of the next.

b) Nitrogen conservation and nutrient recirculation.

Nitrogen loss from dung pads exposed to insects is apparently not high in Kamloops, but dung burial will reduce any loss that does occur. The dung loses much of its moisture when it is incorporated into brood balls in the soil and, moreover, it is held at a relatively constant but lower temperature than on the soil surface. Bacterial action leading to volatilization of ammonia would be reduced but any ammonia that is evolved probably would be adsorbed on soil colloids (Gillard, 1967). Dung pads after deposition undergo intense microbial activity while they are fresh, but as the dung dries this activity is reduced progressively to an extremely slow rate for a very long period of time. Rapid burial of dung

would promote absorption of dung fluids in the soil and as a consequence the initial flush of microbial activity should be impeded. Once below ground, the generally improved conditions (especially increased moisture at certain times and large numbers of soil organisms) for decomposition of organic materials would allow breakdown of the partially dehydrated dung to proceed at a much faster rate than would occur on the surface. Nothing is known about the rate of decomposition of dung in the range soil. It is not known if the cold winter and periodic dry conditions at Kamloops will be serious limiting factors to the incorporation of dung material into soil organic matter, and hence to the recirculation of nutrients. There is no doubt however that it would be more preferable to have fresh dung removed into the soil immediately than to continue under the present conditions.

c) Range plant growth.

Mention has been made already (Chapter III) of the relatively small amounts of N and of other nutrients that are returned by cattle per unit area of range pasture during the grazing season. These quantities nevertheless represent a large proportion of the annual forage production when grazing is intensive. Therefore they should be returned into the soil if it is desired to maintain the productivity of the system. It was shown in Chapter IV that beardless wheatgrass responded very favourably to incorporation of dung into the soil when moisture was not a limiting factor to growth. Other grasses and forbs can be expected to behave similarly. It has taken many years for the rangelands to become degraded to the extent observable in some areas; it would take many more years to rehabilitate them. Efficient dung beetles in the long term could play a

very useful, if inconspicuous, part in this restoration process.

Dung burial not only would be beneficial in rangelands but also in irrigated pastures and in pastures in higher rainfall areas (e.g., Fraser Valley and Vancouver Island). It is not being too optimistic to envisage that beetles selected primarily for the Southern Interior might be able to colonize those other areas. If they do not, other beetle species could be sought specifically for them. The high stocking rates possible in such improved pastures are accompanied by the problems of waste and rejection of forage by cattle due to dung contamination. Breakdown of pads is still inefficient, though much faster than in the rangelands. Dung beetles should minimize those problems. However, the possibility should not be overlooked that areas where dung beetles were active may be especially favourable for weed growth.

Cooperative Introductions.

The literature reveals that an increasing amount of research work is being carried out on dung and the arthropods associated with it. Some areas of the world, including much of North America, apparently have an impoverished native dung beetle fauna in the face of new demands being made on their grassland systems by domestic animals and modern pasture technology. An appreciation of the ecological role of dung beetles and their natural relationships with various mammals means that a number of proposals for introduction of additional beetle species into these regions will probably be made in the future.

The greatest danger to individual introduction programs on large land masses lies in the importation by separate agencies of too many beetle species, each destined for a specific area, but which then colonize more territory than was expected of them originally. It is to

be hoped that a close cooperation can be maintained between the entomologists in any country that undertakes the importation of additional beetles and entomologists in adjoining countries to avoid the unwitting introduction of species that eventually meet and then interact unfavourably.

Unfortunately, the introduction of exotic beetles into new areas is not without its potential hazards. Some beetles are vectors of parasites of domestic and wild animals and are also potential vectors of animal diseases (Fincher et al., 1971). Strictest precautions are therefore necessary when implementing such programs, because release of a parasite or pathogen of any domestic animals could have really disastrous consequences. Moreover, introduced beetles have the potential to carry pathogens affecting themselves or other insects.

APPENDIX I

Insects associated with fresh cattle dung on range and irrigated pasture at Kamloops, B.C.

SPECIES	AUTHORITY*	ORIGIN
ORDER COLEOPTERA		
Histeridae		
HISTER ABBREVIATUS Fabricius	3	Native?
SAPRINUS LUBRICUS Le Conte	3	Native?
SAPRINUS OREGONENSIS Hatch	3	Native
MARGARINOTUS UMBROSUS Casey	3	Native
Hydrophilidae		
CERCYON spp.	11	
SPHAERIDIUM BIPUSTULATUM Fabricius	11	Exotic
SPHAERIDIUM LUNATUM Fabricius	11	Exotic
SPHAERIDIUM SCARABAEOIDES Linnaeus	11	Exotic
Scarabaeidae		
BOREOCANTHON SIMPLEX (Le Conte)	2	Native
ONTHOPHAGUS NUCHICORNIS (Linnaeus)	2	Exotic

* Insects were identified by (1) H.F. Howden, Department of Biology, Carleton University, Ottawa; and the following members of the Taxonomy Section, Entomology Research Institute, Canada Department of Agriculture, Ottawa: (2) E.C. Becker; (3) J.M. Campbell; (4) B. Cooper; (5) L. Forster; (6) J.F. McAlpine; (7) E.E. Lindquist; (8) L. Masner; (9) W.R. Mason; (10) B.V. Peterson; (11) R. de Ruette; (12) G.E. Shewell; (13) H.J. Teskey; (14) J.R. Vockeroth; (15) C.M. Yoshimoto; and (16) the author.

APPENDIX I (continued)

SPECIES	AUTHORITY	ORIGIN
COLEOPTERA (continued)		
Scarabaeidae (continued)		
APHODIUS FOSSOR (Linnaeus)	2	Exotic
APHODIUS FIMETARUIS (Linnaeus)	2	Exotic
APHODIUS CONGREGATUS Mannerheim	1	Native
APHODIUS DISTINCTUS (Mueller)	1	Exotic
APHODIUS GRANARIUS (Linnaeus)	1	Exotic
APHODIUS HAEMORRHOIDALIS (Linnaeus)	1	Exotic
APHODIUS PECTORALIS Le Conte	1	Native
APHODIUS TENELLUS Say	1	Native
APHODIUS VITTATUS Say	1	Native
Staphylinidae		
ALEOCHARA BIMACULATA Gravenhorst	3	Exotic
HYPONYGRUS OBSIDIANUS Melsheimer	3	Native?
ONTHOLESTES CINGULATUS Gravenhorst	3	Native
PHILONTHUS CRUENTATUS Gmelin	3	Exotic
PHILONTHUS DEBILIS Gravenhorst	3	Exotic
PHILONTHUS FUSCIPENNIS Mannerheim	3	Exotic
PHILONTHUS RECTANGULUS Sharp	3	Exotic
**PHILONTHUS SANGUINOLENTUS Gravenhorst	3	Exotic

**First record of this species in Canada.

APPENDIX I (continued)

SPECIES	AUTHORITY	ORIGIN
COLEOPTERA (continued)		
Staphylinidae (continued)		
PLATYSTETHUS AMERICANUS Erichson	3	Native
TACHINUS NIGRICORNIS Mannerheim	3	Native
ORDER DIPTERA		
Ceratopogonidae		
FORCIPOMYIA BREVIPENNIS (Macquart)	5	?
Stratiomyidae		
SARGUS CUPRARIUS (Linnaeus)	10	Exotic
MICROCHRYSA FLAVICORNIS (Meigen)	10	Native
Otitidae		
PHYSIPHORA DEMANDATA (Fabricius)	6	?
Sphaeroceridae		
COPROMYZA ATRA (Meigen)	13	?
LEPTOCERA spp.	13	
Sepsidae		
SEPSIS NEOCYNIPSEA Melander & Spuler	6	?
SALTELLA SPHONDYLII (Schrank)	6	?
Anthomyiidae		
CALYTHEA MICROPTERYX (Thomson)	6	Native

APPENDIX I (continued)

SPECIES	AUTHORITY	ORIGIN
DIPTERA (continued)		
Scatophagidae		
SCATOPHAGA FURCATA (Say)	14	Native
SCATOPHAGA STERCORARIA (Linnaeus)	14	Exotic?
Muscidae		
HAEMATOBIA IRRITANS (Linnaeus)	14	Exotic
HELINA DUPLICATA (Meigen)	14	Exotic
HYDROTAEA ARMIPES (Fallen)	14	Exotic?
MORELLIA MICANS (Macquart)	14	Native
MYOSPILA MEDITABUNDA (Fabricius)	14	Exotic
MUSCA AUTUMNALIS DeGeer	14	Exotic
MUSCA DOMESTICA Linnaeus	16	Exotic?
ORTHELLIA CAESARION (Meigen)	14	Exotic?
PYRELLIA CYANICOLOR (Zetterstedt)	14	Native?
PEGOMYA spp.	6	
Calliphoridae		
EUCALLIPHORA LILAEA (Walker)	4	Native
PHORMIA REGINA (Meigen)	4	Exotic?
Sarcophagidae		
RAVINIA L'HERMINIERI (Robineau-Desvoidy)	4	Native
RAVINIA PLANIFRONS (Aldrich)	12	Native
RAVINIA QUERULA (Walker)	4	Native

APPENDIX I (continued)

SPECIES	AUTHORITY	ORIGIN
ORDER HYMENOPTERA		
Braconidae		
APHAERETA PALLIPES (Say)	9	Native
TRICHOPRIA (subg. PHAENOPRIA): 2 spp.	8	
ASOBARA n.sp.	9	
Cynipidae		
KLEIDOTOMA FOSSA Kieffer	15	Native?
Figitidae		
FIGITES n.sp?	15	
XYALOPHORA QUINQUELINEATA (Say)	15	Native?
MELANIPS ? BILINEATUS (Kieffer)	15	
Pteromalidae		
MUSCIDIFURAX RAPTOR Girault & Saunders	15	?
MUSCIDIFURAX ZARAPTOR Kogan & Legner	15	Native
SPALANGIA HAEMATOBIAE Ashmead	15	Native
ORDER ACARINA		
Pyemotidae (Pygmephorini)		
PEDICULASTER MESEMBRINAE (R. Can.) (associated with HAEMATOBIA IRRITANS (Linnaeus))	7	
Parasitidae		
PARASITUS sp. (associated with APHODIUS FOSSOR (Linnaeus))	7	

APPENDIX I (continued)

SPECIES	AUTHORITY	ORIGIN
ACARINA (continued)		
Macrochelidae		
MACROCHELES GLABER group: sp. near PERGLABER Fil. & Peg. (associated with APHODIUS FOSSOR (Linnaeus))	7	

APPENDIX II

Table 1 Separate anovas for comparison of number of female horn flies trapped at pads both between and within sampling periods and time intervals. Data transformed logarithmically.

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	F-RATIO[a]	PROBABILITY
a) BETWEEN SAMPLING PERIODS AND TIME INTERVALS				
A Sampling period	5	17.546	39.915***	0.000
B Time interval	7	4.452	10.126***	0.000
AB Sampling period x time interval	35	0.508	1.156 ns	0.274
Error	139	0.440		
Total	186	1.063		
b) WITHIN SAMPLING PERIODS				
Sampling period I:				
Time interval	7	1.063	3.918**	0.005

[a] P<0.001 denoted by ***, P<0.01 by **, P<0.05 by * and ns = not significant.

APPENDIX II Table 1 (continued)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	F-RATIO	PROBABILITY
b) WITHIN SAMPLING PERIODS (continued)				
Error	26	0.271		
Total	33	0.439		
Sampling period II:				
Time interval	7	1.685	3.215**	0.012
Error	30	0.524		
Total	37	0.744		
Sampling period III:				
Time interval	7	1.439	2.675*	0.044
Error	18	0.538		
Total	25	0.790		
Sampling period IV:				
Time interval	7	0.653	3.084*	0.027
Error	17	0.212		
Total	24	0.341		

APPENDIX II Table 1 (continued)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	F-RATIO	PROBABILITY
b) WITHIN SAMPLING PERIODS (continued)				
Sampling period V:				
Time interval	7	0.631	1.086 ns	0.403
Error	24	0.581		
Total	31	0.592		
Sampling period VI:				
Time interval	7	1.623	3.508**	0.010
Error	24	0.463		
Total	31	0.725		
c) WITHIN TIME INTERVALS				
Time interval 0000-0300:				
Sampling period	5	2.857	3.944*	0.021
Error	13	0.724		
Total	18	1.317		

APPENDIX II Table 1 (continued)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	F-RATIO	PROBABILITY
c) WITHIN TIME INTERVALS (continued)				
Time interval 0300-0600:				
Sampling period	5	2.759	5.985**	0.006
Error	12	0.461		
Total	17	1.137		
Time interval 0600-0900:				
Sampling period	5	3.789	7.673***	0.000
Error	23	0.494		
Total	28	1.082		
Time interval 0900-1200:				
Sampling interval	5	3.863	12.198***	0.000
Error	22	0.317		
Total	27	0.973		

APPENDIX II Table 1 (continued)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	F-RATIO	PROBABILITY
c) WITHIN TIME INTERVALS (continued)				
Time interval 1200-1500:				
Sampling period	5	2.634	7.381***	0.001
Error	17	0.357		
Total	22	0.874		
Time interval 1500-1800:				
Sampling period	5	2.070	5.470**	0.004
Error	17	0.378		
Total	22	0.763		
Time interval 1800-2100:				
Sampling period	5	1.757	5.492**	0.002
Error	23	0.320		
Total	28	0.576		

APPENDIX II Table 1 (continued)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	F-RATIO	PROBABILITY
c) WITHIN TIME INTERVALS (continued)				
Time interval 2100-2400:				
Sampling period	5	1.896	2.853 ns	0.063
Error	12	0.665		
Total	17	1.027		

APPENDIX II

Table 2 Anova for between treatment comparison of number of adult progeny produced per female horn fly by sampling period and time interval in 1971. Data were transformed to $\sqrt{x+1/2}$.

	SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	F-RATIO	PROBABILITY
A	Treatment (covered vs. exposed)	1	37.061	166.124***	0.000
B	Sampling period	5	1.240	5.560***	0.000
C	Time interval	7	0.952	4.268***	0.001
AB	Treatment x sampling period[a]	5	0.793	3.556**	0.006
AC	Treatment x time interval	7	0.670	3.004**	0.008
BC	Sampling period x time interval	35	0.728	3.263***	0.000
ABC	Treatment x sampling period x time interval[a]	35	0.465	2.086**	0.004
	Error	81	0.223		
	Total	176	0.673		

[a] When the analysis of variance was performed on data from the first 5 sampling periods only, no significant difference was found in the AB and ABC interactions.

APPENDIX II

Table 3 Separate anovas for comparison between and within sampling period and time interval of number of progeny produced per female horn fly by covered and exposed pads in 1971. Data were transformed to $\sqrt{x+1/2}$.

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	F-RATIO	PROBABILITY
a) BETWEEN SAMPLING PERIODS AND TIME INTERVALS				
Covered Pads				
A Sampling period	5	1.754	5.257*	0.001
B Time interval	7	0.979	2.934*	0.014
AB Sampling period x time interval	35	0.553	1.658 ns	0.061
Error	38	0.334		
Total	85	0.556		
Exposed Pads				
A Sampling period	5	0.053	0.487 ns	0.785
B Time interval	7	0.227	2.067 ns	0.067
AB Sampling period x time interval	35	0.209	1.906*	0.022
Error	43	0.110		
Total	90	0.155		

APPENDIX II Table 3 (continued)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	F-RATIO	PROBABILITY
b) WITHIN SAMPLING PERIODS				
Covered Pads				
Sampling period I:				
Time interval	7	0.490	1.635 ns	0.282
Error	5	0.300		
Total	12	0.402		
Sampling period II:				
Time interval	7	1.500	1.651 ns	0.236
Error	9	0.909		
Total	16	1.167		
Sampling periond III:				
Time interval	7	0.491	1.735 ns	0.280
Error	5	0.283		
Total	12	0.404		

APPENDIX II Table 3 (continued)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	F-RATIO	PROBABILITY
b) WITHIN SAMPLING PERIODS (continued)				
Sampling period IV:				
Time interval	7	0.762	19.288*	0.017
Error	3	0.039		
Total	10	0.545		
Sampling period V:				
Time interval	7	0.281	2.287 ns	0.134
Error	8	0.123		
Total	15	0.197		
Sampling period VI:				
Time interval	7	0.197	2.070 ns	0.153
Error	8	0.095		
Total	15	0.140		
Exposed Pads				
Sampling period I:				
Time interval	7	0.397	1.349 ns	0.351

APPENDIX II Table 3 (continued)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	F-RATIO	PROBABILITY
b) WITHIN SAMPLING PERIODS (continued)				
Error	6	0.294		
Total	13	0.345		
Sampling period II:				
Time interval	7	0.068	0.655 ns	0.706
Error	10	0.104		
Total	17	0.090		
Sampling period III;				
Time interval	7	0.200	2.622 ns	0.153
Error	5	0.076		
Total	12	0.148		
Sampling period IV:				
Time interval	7	0.201	2.448 ns	0.171
Error	5	0.082		
Total	12	0.151		

APPENDIX II Table 3 (continued)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	F-RATIO	PROBABILITY
b) WITHIN SAMPLING PERIODS (continued)				
Sampling period V:				
Time interval	7	0.191	3.226 ns	0.062
Error	8	0.059		
Total	15	0.121		
Sampling period VI:				
Time interval	7	0.183	4.130*	0.033
Error	7	0.044		
Total	14	0.109		
c) WITHIN TIME INTERVALS				
Covered Pads				
Time interval 0000-0300:				
Sampling period	5	1.270	6.902 ns	0.132
Error	1	0.184		
Total	6	0.960		

APPENDIX II Table 3 (continued)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	F-RATIO	PROBABILITY
c) WITHIN TIME INTERVALS (continued)				
Time interval 0300-0600:				
Sampling period	5	0.589	1.856 ns	0.322
Error	3	0.317		
Total	8	0.487		
Time interval 0600-0900:				
Sampling period	5	0.896	1.184 ns	0.414
Error	6	0.757		
Total	11	0.820		
Time interval 0900-1200:				
Sampling period	5	0.119	0.444 ns	0.807
Error	8	0.267		
Total	13	0.210		
Time interval 1200-1500:				
Sampling period	5	0.534	1.215 ns	0.437
Error	4	0.440		
Total	9	0.492		

APPENDIX II Table 3 (continued)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	F-RATIO	PROBABILITY
c) WITHIN TIME INTERVALS (continued)				
Time interval 1500-1800:				
Sampling period	5	0.468	3.495 ns	0.080
Error	6	0.134		
Total	11	0.286		
Time interval 1800-2100:				
Sampling period	5	0.308	1.356 ns	0.325
Error	9	0.227		
Total	14	0.256		
Time interval 2100-2400:				
Sampling period	5	0.966	2.594 ns	0.299
Error	1	0.372		
Total	6	0.797		

APPENDIX II Table 3 (continued)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	F-RATIO	PROBABILITY
c) WITHIN TIME INTERVALS (continued)				
Exposed Pads				
Time interval 0000-0300:				
Sampling period	5	0.273	0.831 ns	0.676
Error	1	0.328		
Total	6	0.282		
Time interval 0300-0600:				
Sampling period	5	0.187	0.842 ns	0.620
Error	2	0.223		
Total	7	0.197		
Time interval 0600-0900:				
Sampling period	5	0.117	0.797 ns	0.579
Error	9	0.147		
Total	14	0.136		

APPENDIX II Table 3 (continued)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	F-RATIO	PROBABILITY
c) WITHIN TIME INTERVALS (continued)				
Time interval 0900-1200:				
Sampling period	5	0.117	1.730 ns	0.233
Error	8	0.068		
Total	13	0.086		
Time interval 1200-1500:				
Sampling period	5	0.015	0.087 ns	0.990
Error	6	0.171		
Total	11	0.100		
Time interval 1500-1800:				
Sampling period	5	0.168	7.356*	0.024
Error	5	0.023		
Total	10	0.095		

APPENDIX II Table 3 (continued)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	F-RATIO	PROBABILITY
c) WITHIN TIME INTERVALS (continued)				
Time interval 1800-2100:				
Sampling period	5	0.212	2.201 ns	0.153
Error	8	0.096		
Total	13	0.141		
Time interval 2100-2400:				
Sampling period	5	0.322	7.365*	0.040
Error	4	0.044		
Total	9	0.198		

APPENDIX II

Table 4 Number of horn fly progeny that emerged from covered pads taken during two sampling periods in 1972. Sampling was conducted for only 18 hours in each period. For each time interval the figures given are (moving towards the bottom of the table) : Mean for the interval (retransformed), range of estimates of the mean, and number of observations.

	Mean number of progeny produced per female horn fly					
Sampling period	0300-0600[a]	0600-0900	0900-1200	1200-1500	1500-1800	1800-2100
I (22-24 June)	20.0[b]	7.2	5.4	5.6	6.1	5.3
	18.7-21.3	5.8-9.0	3.8-7.6	3.4-9.8	4.7-7.2	3.2-7.8
	(3)	(3)	(3)	(3)	(3)	(3)
II (21-23 July)	8.8[c]	2.0	4.2	3.7	3.1	3.0
	6.0-14.3	0.3-6.6	2.9-5.4	2.2-5.6	1.3-7.0	1.8-4.5
	(4)	(4)	(5)	(5)	(4)	(4)

[a] Mean in I greater than that in II ($P<0.01$), as measured by a t-test on logarithmically transformed data.

[b] Significantly greater than all other means in the same period ($P<0.001$); no difference between the latter.

[c] Significantly greater than all other means in the same period ($P<0.05$); no difference between the latter.

APPENDIX II

Table 5 Significance of differences between mean number of horn fly progeny that emerged from covered and exposed pads in each time interval in 1971, as indicated by t-tests. Data (transformed to $\sqrt{x+1/2}$ as for the previous anovas) were pooled for all sampling periods after rejection of four aberrant values as described in Chapter I. Data of Fig. 14.

TIME INTERVAL	DEGREES OF FREEDOM	t-VALUE	PROBABILITY
0000-0300	12	2.359*	<0.05
0300-0600	15	5.446***	<0.001
0600-0900	25	4.655***	<0.001
0900-1200	26	5.407***	<0.001
1200-1500	20	4.462***	<0.001
1500-1800	20	5.760***	<0.001
1800-2100	27	4.220***	<0.001
2100-2400	12	2.972**	<0.01

APPENDIX III

Derivation of the formula used in estimating the amount of dung remaining unburied after colonization of dung pads by Onthophagus nuchicornis.

Let DW = dry weight of dung plus soil before ashing, of which

x = dry weight of dung

and y = dry weight of soil;

let AW = dry weight of ashed dung plus soil.

Then for any experimental pad,

(1) $x + y = DW$

dry dung lost 81% of its dry weight on ashing, while soil lost 4%;

therefore,

(2) $0.19x + 0.96y = AW$

multiplying (1) by 0.96 gives

(3) $0.96x + 0.96y = 0.96DW$

subtracting (2) from (3),

$$x = \frac{0.96DW - AW}{0.77}$$

APPENDIX IV

Loss of N from freshly collected dung when oven-dried at various temperatures on different occasions during 1972. All dried samples weighed 250 g initially.
All determinations made by the micro-Kjeldahl method and figures shown have been corrected to give an estimate of true N percentage (observed %N x 1.163).

Date of Analysis	Mean per cent N (dry weight basis)*					Fresh N%-dry N%	% loss on drying
	Fresh dung	Dry dung					
		Dried 50°C	Dried 70°C	Dried 100°C	Mean		
21 June	2.27(9)	---	---	2.04(4)	2.04	0.23	10.1
4 July	2.33(10)	2.12(7)	---	2.13(7)	2.13	0.20	8.6
1 August	2.47(4)	---	2.31(2)	2.30(2)	2.31	0.16	6.5
5 August	2.23(6)	---	2.05(4)	---	2.05	0.18	8.1

* Brackets indicate the number of samples analyzed in each case; more samples were used for fresh dung because of the inherent heterogeneity of this material in comparison with dry powdered dung.

REFERENCES CITED

Aksinin, J.S. 1929. The output of free ammonia by house-fly larvae (Musca domestica L.). Plant Protection 6:379-382. Cited by L.S. West. 1951. The housefly. Comstock Publishing Co., Ithaca, New York. 584 pp.

Anderson, J.R. 1966. Biological interrelationships between feces and flies. Pages 20-23 in Proc. Am. Soc. Agric. Eng. Symp. on Management of Farm Animal Wastes. Am. Soc. Agric. Eng. Publ. No. SP-0366.

Balthasar, V. 1963a. Monographie der Scarabaeidae und Aphodiidae der palaearktischen und orientalischen Region. Coleoptera: Lamellicornia. Band 1. Scarabaeinae and Coprinae (Pinotini, Coprini). Tschech. Akad. Wissenschaften, Prag. 391 pp.

Balthasar, V. 1963b. Monographie der Scarabaeidae und Aphodiidae der palaearktischen und orientalischen Region. Coleoptera: Lamellicornia. Band 2. Coprinae (Onitini, Oniticellini, Onthophagini). Tschech. Akad. Wissenschaften, Prag. 627 pp.

Banfield, A.W.F., and N.S. Novakowski. 1960. The survival of the Wood Bison (Bison bison athabascae Rhoads) in the Northwest Territories. Nat. Mus. Can. Nat. Hist. Pap. 8. 6 pp.

Barrow, N.J. 1967. Some aspects of the effects of grazing on the nutrition of pastures. J. Aust. Inst. Agric. Sci. 33: 254-262.

Baumberger, J.P. 1919. A nutritional study of insects, with special reference to the microorganisms and their substrata. J. Exp. Zool. 28: 1-81.

Bay, D.E., C.W. Pitts, and G. Ward. 1970. Face fly larval development in relation to bovine sex and quantity of feces. J. Econ. Entomol. 63: 1973.

Blume, R.R. 1970. Insects associated with bovine droppings in Kerr and Bexar Counties, Texas. J. Econ. Entomol. 63: 1023-1024.

Blume, R.R., S.E. Kunz, B.F. Hogan, and J.J. Matter. 1970. Biological and ecological investigations of horn flies in Central Texas: Influence of other insects in cattle manure. J. Econ. Entomol. 63: 1121-1123.

Bornemissza, G.F. 1960. Could dung-eating insects improve our pastures? J. Aust. Inst. Agric. Sci. 26: 54-56.

Bornemissza, G.F. 1968. Studies on the histerid beetle Pachylister chinensis in Fiji, and its possible value in the control of buffalo-fly in Australia. Aust. J. Zool. 16: 673-688.

Bornemissza, G.F. 1969. A new type of brood care observed in the dung beetle Oniticellus cinctus (Scarabaeidae). Pedobiologia 9: 223-225.

Bornemissza, G.F. 1970. Insectary studies on the control of dung breeding flies by the activity of the dung beetle, Onthophagus gazella F. (Coleoptera: Scarabaeinae). J. Aust. Entomol. Soc. 9: 31-41.

Bornemissza, G.F., and C.H. Williams. 1970. An effect of dung beetle activity on plant yield. Pedobiologia 10: 1-7.

Brown, A.W.A. 1936. The excretion of ammonia and uric acid during the larval life of certain muscoid flies. J. Exp. Biol. 13: 131-139.

Brown, A.W.A. 1938. The nitrogen metabolism of an insect (Lucilia sericata Mg.) II. Ammonia and other metabolites. Biochem. J. 32: 903-912.

Brown, W.J. 1940. Notes on the American distribution of some species of Coleoptera common to the European and North American continents. Can. Entomol. 72: 65-78.

Bruce, W.G. 1964. The history and biology of the horn fly, Haematobia irritans (Linnaeus); with comments on control. N.C. Agric. Exp. Stn Tech. Bull. 157. 32 pp.

Burmeister, F. 1930. Die Brutfursorge und das Bauprinzip der Gattung Onthophagus Latreille. Z. Morphol. Oekol. Tiere, Berlin, 16: 559-647.

Canada Department of Agriculture. 1971. Roundup of range fertilization research in British Columbia, Alberta, and Oregon. Unpublished mimeo. Report on Rangeland Fertilization Meeting. Research Station, Kamloops, B. C. 36 pp.

Coffey, M.D. 1966. Studies on the association of flies (Diptera) with dung in Southeastern Washington. Ann. Entomol. Soc. Am. 59: 207-218.

Combs, R.L., Jr., and C.E. Hoelscher. 1969. Hymenopterous pupal parasitoids found associated with the horn fly in Northeast Mississippi. J. Econ. Entomol. 62: 1234-1235.

Commonwealth Scientific and Industrial Research Organization, Australia (CSIRO). 1969. Northern cattle pest. Rural Research in CSIRO No. 65: 9-10.

Commonwealth Scientific and Industrial Research Organization, Australia (CSIRO). 1970. Division of Entomology: Annual Report for 1969-70. Canberra, A.C.T.

Commonwealth Scientific and Industrial Research Organization, Australia (CSIRO). 1972. Division of Entomology: Annual Report for 1971-72. Canberra, A.C.T.

Cowan, I. McT. 1940. Distribution and variation in the native sheep of North America. Am. Midl. Nat. 24: 505-580.

Cowan, I. McT., and C.J. Guiget. 1965. The mammals of British Columbia. B.C. Provincial Mus. Handbook No. 11, Victoria, British Columbia. 414 pp.

Creelman, I.S., ed. 1967. Pests of mammals and birds. Can. Insect Pest Rev. 45: 15.

Darlington, P.J., Jr. 1957. Zoogeography: The geographical distribution of animals. John Wiley and Sons, New York. 675 pp.

Daubenmire, R. 1970. Steppe vegetation of Washington. Washington Agric. Exp. Stn Tech. Bull. 62. 131 pp.

Davidson, R.L. 1964. Theoretical aspects of nitrogen economy in grazing experiments. J. Br. Grassl. Soc. 19: 273-280.

Depner, K.R. 1961. The effect of temperature on the development and diapause of the horn fly, Siphona irritans (L.) (Diptera:Muscidae). Can. Entomol. 93: 855-859.

Depner, K.R. 1962. Continuous propagation of the horn fly, Haematobia irritans (L.) (Diptera: Muscidae). Can. Entomol. 94: 893-895.

Depner, K.R. 1968. Hymenopterous parasites of the horn fly, Haematobia irritans (Diptera: Muscidae), in Alberta. Can. Entomol. 100: 1057-1060.

Depner, K.R. 1969. Distribution of the face fly, Musca autumnalis (Diptera: Muscidae), in Western Canada and the relation between its environment and population density. Can. Entomol. 101: 97-100.

Dowding, V.M. 1967. The function and ecological significance of the pharyngeal ridges occurring in the larvae of some cyclorrhaphous Diptera. Parasitology 57: 371-388.

Ferrar, P., and J.A.L. Watson. 1970. Termites (Isoptera) associated with dung in Australia. J. Aust. Entomol. Soc. 9: 100-102.

Fincher, G.T., R. Davis, and T.B. Stewart. 1971. Flight activity of coprophagous beetles on a swine pasture. Ann. Entomol. Soc. Am. 64: 855-860.

Finne, D., and M. Desiere. 1971. Etude Synecologique des bouses de Bovides. 1. Evolution estivale de la biomasse des Coleopteres en fonction du vieillissement des bouses. Rev. Ecol. Biol. Sol. 8: 409-417.

Fullaway, D.T. 1921. Horn fly control. Hawaii Forest. and Agric. 18: 219-221.

Gillard, P. 1967. Coprophagous beetles in pasture ecosystems. J. Aust. Inst. Agric. Sci. 33: 30-34.

Greenham, P.M. 1972. The effects of the variability of cattle dung on multiplication of the bushfly (Musca vetustissima Walk.) J. Anim. Ecol. 41: 153-165.

Hafez, M. 1939. The life history of Sphaeridium scarabaeoides L. (Coleoptera: Hydrophilidae). Bull. Soc. Fouad. Ier Entomol. 23: 312-318.

Halffter, G., and E.G. Matthews. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). Folia Entomol. Mex. Nos. 12-14: 1-312.

Hammer, O. 1941. Biological and ecological investigations on flies associated with pasturing cattle and their excrement. Reprinted from Vidensk. Medd. Dan. Naturhist. Foren. Kbh. 105. Bianco Lunos Bogtrykkeri A/S, Copenhagen. 257 pp.

Hargett, L.T., and R.L. Goulding. 1962. Studies on the behavior of the horn fly Haematobia irritans (Linn.). Oreg. Agric. Exp. Stn Tech. Bull. 61. 27 pp.

Harris, R.L. and E.D. Frazar. 1970. Intake of blood by adult horn flies reared in the laboratory. Ann. Entomol. Soc. Am. 63: 1475-1476.

Hatch, M.H. 1953. The beetles of the Pacific Northwest. Part I: Introduction and Adephaga. University of Washington Press, Seattle, Washington. 340 pp.

Hatch, M.H. 1971. The beetles of the Pacific Northwest. Part V: Rhipiceroidea, Sternoxi, Phytophaga, Rhynchophora, and Lamellicornia. University of Washington Press, Seattle, Washington. 662 pp.

Hiller, A., J. Plazin, and D.D. van Slyke. 1948. A study of conditions for Kjeldahl determination of nitrogen in proteins. Description of methods with mercury as catalyst, and titimetric and gasometric measurements of the ammonia formed. J. Biol. Chem. 176: 1401-1420.

Hoelscher, C.E., and R.L. Combs, Jr. 1971. The horn fly. 1. Seasonal incidence of diapause in Mississippi. J. Econ. Entomol. 64: 256-259.

Howden, H.F. 1966. Some possible effects of the Pleistocene on the distributions of North American Scarabaeidae (Coleoptera). Can. Entomol. 98: 1177-1190.

Howden, H.F., and O.L. Cartwright. 1963. Scarab beetles of the genus Onthophagus Latreille north of Mexico (Coleoptera: Scarabaeidae). Proc. U.S. Natl. Mus. 114: 1-135.

Hubbard, W.A., and J.L. Mason. 1967. Residual effects of ammonium nitrate and ammonium phosphate on some native ranges of British Columbia. J. Range Manage. 20: 1-5.

Hutton, J.B., K.E. Jury, and E.B. Davies. 1967. Studies of the nutritive value of New Zealand dairy pastures. V. The intake and utilization of potassium, sodium, calcium, phosphorus and nitrogen in pasture herbage by lactating dairy cattle. N.Z.J. Agric. Res. 10: 367-388.

Kessler, H., and E.U. Balsbaugh, Jr. 1972. Succession of adult Coleoptera in bovine manure in east central South Dakota. Ann. Entomol. Soc. Am. 65: 1333-1336.

Kunz, S.E., R.R. Blume, B.F. Hogan, and J.J. Matter. 1970. Biological and ecological investigations of horn flies in central Texas: Influence of time of manure deposition on oviposition. J. Econ. Entomol. 63: 930-933.

Kunz, S.E., B.F. Hogan, R.R. Blume and J.L. Eschle. 1972. Some bionomical aspects of horn fly populations in central Texas. Environmental Entomol. 1: 565-568.

Lake, G.R., R. McCutchan, R. van Meter, and J.C. Neel. 1951. Effects of digestion temperature on Kjeldahl analyses. Anal. Chem. 23: 1634-1638.

Larsen, E.B., and Thomsen, M. 1940. Vidensk. Medd. Dan. Naturhist. Foren. Kbh. 104: 1-75. Cited by P.S. Messenger. 1959. Bioclimatic studies with insects. Ann. Rev. Entomol. 4: 183-206.

Laurence, B.R. 1954. The larval inhabitants of cow pats. J. Anim. Ecol. 23: 234-260.

Lengerken, H. von. 1954. Die Brutfursorge and Brutpflegeinstinkte der Kafer. Akademische Verlagsgesellschaft, Geest and Portig K.-G., Leipzig. 383 pp.

Lindquist, A.W. 1933. Amounts of dung buried and soil excavated by certain Coprini (Scarabaeidae). J. Kansas Entomol. Soc. 6: 109-125.

Lindquist, A.W. 1935. Notes on the habits of certain coprophagous beetles and methods of rearing them. U.S. Dep. Agric. Circ. 351: 1-10.

Lindquist, A.W. 1936. Parasites of horn fly and other flies breeding in dung. J. Econ. Entomol. 29: 1154-1158.

Lindroth, C.H. 1957. The faunal connections between Europe and North America. John Wiley and Sons, New York. 344 pp.

Lotero, J., W.W. Woodhouse, Jr., and R.G. Petersen. 1966. Local effect on fertility of urine voided by grazing cattle. Agron.J. 58: 262-265.

MacDiarmid, B.N., and B.R. Watkin. 1972. The cattle dung patch. 2. Effect of a dung patch on the chemical status of the soil and ammonia losses from the patch. J. Br. Grassl. Soc. 27: 43-48.

MacFadyen, A. 1961. Metabolism of soil invertebrates in relation to soil fertility. Ann. Appl. Biol. 49: 215-218.

MacFadyen, A. 1964. Energy flow in ecosystems and its exploitation by grazing. Pages 3-20 in D.J. Crisp, ed. Grazing in terrestrial and marine environments. Blackwell, Oxford.

MacNay, C.G., ed. 1959. Livestock conditions in British Columbia in 1958. Can. Insect Pest Rev. 37: 21.

Marsh, R., and R.C. Campling. 1970. Fouling of pastures by dung. Herbage Abstracts 40: 123-130.

Mason, V.C. 1969. Some observations on the distribution and origin of nitrogen in sheep faeces. J. Agric. Sci., Cambridge. 73: 99-111.

Mason, J.L., and J.E. Miltimore. 1959. Increase in yield and protein content of native bluebunch wheatgrass from nitrogen fertilization. Can. J. Plant Sci. 39: 501-504.

Mason, J.L. and J.E. Miltimore. 1964. Effect of nitrogen content of beardless wheatgrass on yield response to nitrogen fertilization. J. Range Manage. 17: 145-147.

Mason, J.L., and J.E. Miltimore. 1969. Yield increases from nitrogen on native range in Southern British Columbia. J. Range Manage. 22: 128-131.

Mason, J.L., and J.E. Miltimore. 1972. Ten year yield response of beardless wheatgrass from a single nitrogen application. J. Range Manage. 25: 269-272.

McLean, A., and L.S. Marchand. 1968. Grassland ranges in the Southern Interior of British Columbia. Can. Dep. Agric. Publ. 1319. 28 pp.

McLean, A., and E.W. Tisdale. 1972. Recovery rate of depleted range sites under protection from grazing. J. Range Manage. 25: 178-184.

McLintock, J., and K.R. Depner. 1954. A review of the life-history and habits of the horn fly, Siphona irritans (L.) (Diptera: Muscidae). Can. Entomol. 86: 20-23.

Messenger, P.S. 1959. Bioclimatic studies with insects. Ann. Rev. Entomol. 4: 183-206.

Miller, A. 1954. Dung beetles (Coleoptera, Scarabaeidae) and other insects in relation to human feces in a hookworm area of Southern Georgia. Am. J. Trop. Med. Hyg. 3: 372-389.

Miller, A. 1961. The mouth parts and digestive tract of adult dung beetles (Coleoptera: Scarabaeidae) with reference to the ingestion of helminth eggs. J. Parasitol. 47: 735-744.

Miller, R.W. 1970. Larvicides for fly control - a review. Bull. Entomol. Soc. Am. 16: 154-158.

Miltimore, J.E., J.L. Mason, and C.B.W. Rogers. 1962. Increase in seed production from nitrogen fertilization of native beardless wheatgrass. Can. J. Plant Sci. 42: 359-364.

Mohr, C.O. 1943. Cattle droppings as ecological units. Ecol. Monogr. 13: 275-298.

Neilson, C.L. 1955. Handbook of the main economic insects of British Columbia. Part II. Livestock insects. Unpublished mimeo. British Columbia Department of Agriculture. 40 pp.

Norman, M.J.T., and J.O. Green. 1958. The local influence of cattle dung and urine upon the yield and botanical composition of permanent pasture. J. Br. Grassl. Soc. 13: 39-45.

Osborne, D. 1953. Archaeological occurrences of pronghorn antelope, bison, and horse in the Columbia Plateau. Sci. Monthly 77: 260-269.

Papp, L. 1970. Ecological and production biological data on the significance of flies breeding in cattle droppings. Acta Zool. Acad. Sci. Hung. 17: 91-105.

Pemberton, C.E. 1935. Entomology. Pages 19-26 in Rep. Comm. Exp. Sta. Hawaii. Sug. Pl. Ass. for 1934, Honolulu, Hawaii. Cited in Rev. Appl. Entomol. (B), 23: 173.

Percival, J. 1910. Agricultural bacteriology. Duckworth & Co., London. 408 pp.

Perrin, C.H. 1953. Rapid modified procedure for determination of Kjeldahl nitrogen. Anal. Chem. 25: 968-971.

Petersen, R.G., W.W. Woodhouse, Jr., and H.L. Lucas. 1956. The distribution of excreta by freely grazing cattle and its effect on pasture fertility: II. Effect of returned excreta on the residual concentration of some fertilizer elements. Agron. J. 48: 444-449.

Peterson, A. 1964. Entomological techniques. How to work with insects. 10th ed. Edwards Bros., Ann Arbor, Michigan. 435 pp.

Poorbaugh, John Harvey, Jr. 1966. Ecological studies on the insect community utilizing undisturbed cattle droppings. Ph. D. Thesis. University of California, Berkeley. 157 pp. University Microfilms, Ann Arbor, Mich. (Diss. Abstr. 28: 224-B).

Poorbaugh, J.H., J.R. Anderson, and J.F. Burger. 1968. The insect inhabitants of undisturbed cattle droppings in Northern California. Calif. Vector Views 15(3) : 17-36.

Power, J.F. 1970. Nitrogen management of semi-arid grasslands in North America. Proc. XI Int. Grassland Congress, 1970: 468-471.

Power, J.F. 1972. Fate of fertilizer nitrogen applied to a Northern Great Plains rangeland ecosystem. J. Range Manage. 25: 367-371.

Protsenko, A.I. 1968. Lamellicorn beetles of the Kirgiz (Coleoptera, Scarabaeidae). Ilim, Frunze, Kirgizia. 311 pp. (in Russian).

Ritcher, P.O. 1966. White grubs and their allies. Studies in entomology No. 4, Oregon State University Press, Corvallis, Oregon. 219 pp.

Roe, F.G. 1970. The North American buffalo. A critical study of the species in its wild state. 2nd ed. University of Toronto Press, Toronto. 991 pp.

Russell, E.W. 1961. Soil conditions and plant growth. Longmans, Green and Co., London. 688 pp.

Sanders, D.P., and R.C. Dobson. 1966. The insect complex associated with bovine manure in Indiana. Ann. Entomol. Soc. Am. 59: 955-959.

Sanders, D.P., and R.C. Dobson. 1969. Contributions to the biology of the horn fly. J. Econ. Entomol. 62: 1362-1366.

Scheffe, H. 1959. The analysis of variance. John Wiley and Sons, New York. 477 pp.

Sokal, R.R., and F.J. Rohlf. 1969. Biometry. Freeman and Co., San Francisco, California. 776 pp.

Spilsbury, R.H., and E.W. Tisdale. 1944. Soil-plant relationships and vertical zonation in the Southern Interior of British Columbia. Sci. Agr. 24: 395-436.

Steel, R.G.D., and J.H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., New York. 481 pp.

Teichert, M. 1959. Die Bodenbiologische Bedeutung der coprophagen Lamellicornier. Wiss. Z. Martin Luther University Halle-Wittenberg Math. -Naturwiss. Reihe 8: 879-882.

Teskey, H.J. 1969. On the behaviour and ecology of the face fly, Musca autumnalis (Diptera: Muscidae). Can. Entomol. 101: 561-576.

Thomas, G.D., and C.E. Morgan. 1972a. Parasites of the horn fly in Missouri. J. Econ. Entomol. 65: 169-174.

Thomas, G.D., and C.E. Morgan. 1972b. Field-mortality studies of the immature stages of the horn fly in Missouri. Environmental Entomol. 1: 453-459.

Thomas, G.D., and B. Puttler. 1970. Seasonal parasitism of the face fly by the nematode Heterotylenchus autumnalis in central Missouri, 1968. J. Econ. Entomol. 63: 1922-1923.

Thomas, G.D., B. Puttler, and C.E. Morgan. 1972. Further studies of field parasitism of the face fly by the nematode Heterotylenchus autumnalis in central Missouri, with notes on the gonadotrophic cycles of the face fly. Environmental Entomol. 1: 759-763.

Tisdale, E.W. 1947. The grasslands of the Southern Interior of British Columbia. Ecology 28: 346-382.

Tisdale, E.W., A. McLean, and S.E. Clarke. 1954. Range resources and their management in British Columbia. J. Range Manage. 7: 3-9.

Treherne, R.C., and E.R. Buckell. 1924. The grasshoppers of British Columbia. Can. Dep. Agric. Bull. 39. 40 pp.

U.S. Department of Agriculture (USDA). 1965. Losses in agriculture. U.S. Dep. Agric. Agric. Handb. 291. 120 pp.

Valiela, I. 1969. An experimental study of the mortality factors of larval Musca autumnalis DeGeer. Ecol. Monogr. 39: 199-225.

Vockeroth, J.R. 1953. Musca autumnalis DeG. in North America (Diptera: Muscidae). Can. Entomol. 85: 422-423.

Voris, R. 1936. The rapid spread of an European Staphylinid in North America (Coleoptera, Staphylinidae). Ann. Entomol. Soc. Am. 29: 78-80.

Walker, E.P. 1968. Mammals of the world. 2nd ed. Vol. II. John Hopkins Press, Baltimore, Md. 853 pp.

Walter, H., and H. Lieth. 1964. Klimadiagramm-Weltatlas. 2. Lieferung. VEB Gustav Fischer Verlag, Jena. Loose-leaf pub. n.p.

Walter, H., and H. Lieth. 1967. Klimadiagramm-Weltatlas. 3. Leiferung. VEB Gustav Fischer Verlag, Jena. Loose-leaf pub. n.p.

West, L.S. 1951. The housefly. Its natural history, medical importance, and control. Comstock Publishing Co., Ithaca, New York. 584 pp.

Whitehead, D.C. 1970. The role of nitrogen in grassland productivity. A review of information from temperate regions. Commonwealth Bureau Past. Field Crops Bull. 48, Commonwealth Agr. Bureaux, Bucks, England. 202 pp.

Wolcott, G.N. 1922. Insect parasite introduction in Porto Rico. J. Dep. Agric. Porto Rico 6: 5-20. Cited by G. Halffter and E.G. Matthews. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). Folia Entomol. Mex. Nos. 12-14: 1-312.

CURRICULUM VITAE

Angus Macqueen

Personal History:

Place of birth: Warwick, Queensland, Australia

Date of birth: December 8, 1939

Marital Status: Married, no children

Educational Background:

1949-1953 Primary education in Toowoomba, Queensland

1954-1957 Secondary education at Church of England Grammar School, Brisbane. Matriculation to University of Queensland.

Degrees:

1962 Bachelor of Agricultural Science - University of Queensland
Final year major subject - Soil Science

1967 Master of Agricultural Science - University of Queensland

Awards:

Commonwealth Scholarship at University of Queensland, 1958-1961

Graduate Associate, Simon Fraser University, 1970-1973

Simon Fraser University President's Research Grant, Summer 1971 and 1972

Teaching Experience:

1963-1964 Teaching Fellow, Department of Entomology, University of Queensland. Entomology.

1965-1966 Demonstrator, Department of Entomology, University of Queensland.

1970-1972 Graduate Associate, Department of Biological Sciences, Simon Fraser University. Introductory Biology, Entomology, Pestology, Biosystematics.

Research Experience:

1962 Research Fellow (Soil Physics), Department of Agriculture, University of Queensland.

1964-1966 Masters Degree
Thesis title: A Comparative Study of the Biology and Immature Stages of Two Species of Myrmecia (Hymenoptera: Formicidae).

1966-1969 Entomologist with Bureau of Sugar Experiment Stations, Gordonvale, Queensland. Promoted to Research Entomologist, 1969.

Membership in Professional Organizations:

Australian Entomological Society
Queensland Entomological Society
Australian Institute of Agricultural Science

Publications:

Notes on the large moth borer, Bathytricha truncata (Walker). Proc. Qld. Soc. Sugar Cane Technol. 36: 57-65.