THE BIO-ECOLOGY AND CONTROL OF *COPROICA VAGANS* AND *COPROICA HIRTULA* (DIPTERA: SPHAEROCERIDAE) IN CATTLE FEEDLOTS

by

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TABLE OF CONTENT

CHAPTER 1

GENERAL INTRODUCTION AND LITERATURE REVIEW

When vertebrates evolved onto land, insects were already a well-established terrestrial group. The vertebrates offered many new food resources in the form of blood, dung, fur, secretions, skin and waste food (Strong, 1992). Although some insects were committed to life styles from which they could not capitalise on such resources, other species developed close associations with vertebrates, often using their dung (Strong, 1992). This valuable source of nutrition has been exploited by several insects, particularly Coleoptera and Diptera, where entire larval lives are spent feeding on dung (Hammer, 1941). Several authors recorded different Diptera and Coleoptera species living in the dung of vertebrates *e.g.* Hafez, 1939; Hammer, 1941; Mohr, 1943; Laurence, 1954; Poorbaugh, 1966; Blume, 1970; Papp, 1976; Merritt & Anderson 1977 and Rohacèk, 1982. According to Hammer (1941), the diversity of Diptera in dung is as extensive as the Coleoptera, and together with a large number of Hymenoptera, Collembola, Acarina, Myriapoda, Oligochaeta, Nematoda and micro-organisms, they form a cosmopolitan group of invertebrates and micro-organisms inhabiting field droppings. From this it is clear that a cow dung pat can form a biotope on its own. Mohr (1943) even described cattle droppings as an ecological unit during studies that he conducted in the USA.

The Sphaeroceridae, or "lesser dung flies", is a large and easily recognizable family. They are tiny to medium-sized acalyptrate flies. Most species are dull black to dark brown, although they may be shiny on certain body parts, and a few species have part or the entire face and frons yellow or reddish brown (Pitkin, 1989). They are between 0.8 mm and 7 mm in length and run, flit or hop actively over the dung surface and spend most of their time in the crevices and galleries in the dung (Mohr, 1943). Some Sphaeroceridae species are apterous (Papp, 1982; Norrbom & Kim, 1985; Papp, 1988), and a remarkably high number of sphaerocerids are brachypterous (de Coninck, 1985).

Sphaeroceridae are mainly diurnal, although some species are reported to have nocturnal habits (Richards, 1930). Although very little is available in the literature on the biology of Sphaeroceridae, the taxonomy of this family has been thoroughly researched by several authors, including Richards, 1930; Collin, 1956; Okely, 1974; Papp, 1979a, Rohacèk, 1982; de Coninck, 1985; Pitkin, 1989. The only available literature on the biology of Sphaeroceridae are publications by Hafez (1949) who studied *Coproica ferruginata* (Stenhammer), Fredeen & Glen (1970) who investigated *Leptocera caenosa* (Rondani) and Lachmann (1991) who compared the life cycles of two species, *Coproica lugubris* (Haliday) and *Chaetopodella scuttelaris* (Haliday) in Germany.

All species of Sphaeroceridae are generally saprophagous, their larvae developing in decaying organic matter (Pitkin, 1986). Based on a review of foreign and British literature, Skidmore (1931) listed 61 species of Sphaeroceridae, associated with dung, manure, privies or sewage. Twelve of these species were recorded breeding in cattle dung and a further 10 species breeding in horse dung. Despite their common name, not all lesser dung flies feed and breed on dung. Different species have different habitat preferences and breed in different types of decaying organic matter. According to Rohacèk (1982), many species may fall into more than one category, although some are more restricted as far as their habitat preferences are concerned. According to the feeding substrate preferences of larvae and adults, Rohacèk (1982) placed the different species into several categories, namely phytosaprophagous, fungivorous, necrophagous, coprophagous or polysaprophagous, although there is still doubt as to whether they consume decaying organic remains directly or the micro-organisms in the medium causing decay.

Some species, *e.g. Toracochaeta zosterae* (Haliday) (Sphaeroceridae) are found at the coast where they are detritivores on decaying seaweed (Phillips & Arthur, 1994). Most decay cycles such as the wrack cycle (of seaweed) are mediated by sphaerocerid-dominated insect communities (Marshall, 1982). Chown (1996) also found a

brachypterous sphaerocerid, *Antrops truncipennis* Enderlein to be an obligate feeder on stranded seaweeds in the supralittoral zone on subantarctic islands of the South Indian Ocean. *Leptocera* (*Rachispoda*) sp. and *Opacifrons* sp. are associated with ponds, streams and rivers, where their larvae probably develop in mud (Richards, 1930). *Halidayina spinipennis* (Haliday) and other sphaerocerids are frequently caught amongst decaying grass cuttings (Pitkin, 1989). Okely (1974) successfully reared numerous species from decaying grass cuttings used as bait in rabbit burrows. *Kimosina* (*Alimosina*) *empirica* (Hutton) is a necrophagous species known to breed in the decaying flesh of humans, seals and rabbits (Pitkin, 1989). Some species are kleptoparasitic and phoretic (Sivinski, 1983). Moreover, Smith (1975) listed 10 species from fox corpses in London; Dear (1968) recorded 12 species on carrion in Europe while Richards (1930) found two species from dead snails in tropical Africa. *Pullimosina heteroneura* (Haliday) has been reared from cultivated mushrooms (Austin, 1937) while *Opalimosina* (*Hackmanina*) *czernyi* (Duda) and *Spelobia* (*Spelobia*) *parapusio* (Dahl) are typical fungivorous species (Rohacèk, 1982). Sphaeroceridae have been implicated as the major means by which nematodes are disseminated among mushroom houses, and they occasionally reached nuisance levels in food-processing plants and other buildings (Haglund & Milne, 1973). Chandler (1990) collected both *Coproica vagans* (Haliday) and *Coproica hirtula* (Rondani) from decaying fungi, but indicated that the genus *Coproica* cannot be considered as true fungus feeders. A species in America has even been involved in a case of human intestinal myiasis (Micks & McKibben, 1956).

Pitkin (1989) has demonstrated that many dung and carrion-feeding species also have a preference for a particular habitat. Quite a number of sphaerocerids have been recorded from runs and nests of small mammals (Richards, 1930; Davis, 1934; Judd, 1961; Hackman, 1969) which often contain dung and decaying plant material. As their microbe-associated habits suggest, sphaerocerids carry many pathogenic microorganisms, although their reclusive habits preclude a major role in disease

transmission (Greenham, 1971). Payne (1982) recorded several species from the entrance of badger nests. Richards (1930) also noted a few species in the nests of bees, wasps and ants and in some caves. In Southern Europe, north and central Africa, Sri Lanka, Australia and central and north America a number of species are associated with dung-rolling scarab beetles (Richards, 1930; Sivinski, 1983). Pitkin (1986) also stated that puparia are frequently found during archaeological excavations.

The Sphaeroceridae have a worldwide distribution and more than 1000 species have been described in three subfamilies Copromyzinae, Sphaerocerinae and Limosininae (Pitkin, 1989). A number of these are synanthropous (Hackman, 1969) and occur wherever man and domestic animals have become established (Pitkin, 1989). There are about 120 species recorded from the Neartic Region (Richards, 1980), 173 species from the Neotropical Region (Richards, 1960), 295 species from the Afrotropical Region (Richards, 1980), 70 species from the Oriental Region (Hackman, 1969) and 270 species from the Palaeartic Region (Papp, 1976). The Australiasian, Oceanian and Antarctic Regions have not yet been catalogued, but there are about 20 species recorded from New Zealand (Harrison, 1959) and 22 species from Hawaii (Tenorio, 1968).

At the current study area near Harrismith, two species of Sphaeroceridae present were *C. vagans* and *C. hirtula*. The wide distribution of *C. vagans* and *C. hirtula* is reflected in Table 1.1. According to Papp (1979a), *C. vagans* and *C. hirtula* occur only in subtropical and infrequently in tropical territories, where the melanin-synthesis in the cycle of the imagoes is interrupted by climatic factors. It is not clear what Papp (1979a) meant by this latter statement, but it is possible that the imagoes in tropical territories have less pigment deposition compare to those in subtropical regions.

Coproica species are relatively well known and the descriptions of species dating from the last century were revised by Duda in 1918 (Papp, 1979a). Collin (1956) and Richards (1960) also made valuable contributions to our knowledge of species of the genus

Coproica. Richards (1980) listed three *Coproica* species that are present in South Africa. They are *C. ferruginata*, *Coproica pseudolugubris* (Duda) and *C. vagans*. These species were recorded from Kleinmond in the Western Cape and Hilton Road and Kokstad in KwaZulu-Natal (Richards, 1980). Succession studies that were conducted over a period of eight seasons revealed that further Sphaeroceridae species are present in the Free State (see Chapter 2). Larvae and imagoes of most *Coproica* species are coprophagous, *e.g. Coproica coreana* Papp, *Coproica digitata* (Duda), *Coproica dentata* Papp, *Coproica ghanensis* Papp, *C. lugubris* and *C. pseudolugubris*, which all develop in the droppings of domestic and wild ungulates (Papp, 1979a).

Table 1.1: World distribution of *Coproica vagans* and *Coproica hirtula*.

1. Southeastern Washington, USA (Coffey, 1966)
2. Northern California, USA (Poorbaugh *et al.*, 1968)
3. Kent, London, Essex, Herts, Hants, Bucks, Berks, Cornwall, Northfolk, Oxon, Wilts, Lundy, Suffolk, Cambs, N. Wales, Westmoreland, Hunts, Hereford, Great Britain (Pitkin, 1989).
4. Ireland (Richards, 1980)
5. Central Solvakia, (Rohacèk, 1983).
6. Hungary (Papp, 1979a).
7. Novi, Yugoslavia. (Papp, 1979a).
8. Csik, Romania. (Papp, 1979a).
9. Carlopago, Italy. (Papp, 1979a).
10. Dushanbe, Tadzhikistan. (Papp, 1979a).
11. Afghanistan. (Papp, 1979a).
12. Mongolia. (Papp, 1979a).
13. Azapa, Chile. (Papp, 1979a).
14. Gabes, Tunisia. (Papp, 1979a).
15. Ethiopia (Richards, 1980)
16. St. Helena (Richards, 1980)
17. Canary Islands (Richards, 1980)
18. Tanzania (Richards, 1980)
19. Democratic Republic of Congo (Richards, 1980)

Certain species *e.g. C. vagans* and *C. ferruginata* live in large numbers in all countries where stock-breeding has reached an advanced stage, and in view of their way of life, man has contributed considerably to the spreading of certain *Coproica* species (Papp, 1979a). Introduction of such Sphaeroceridae species into South Africa probably occurred through importing cattle from Europe (Hackman, 1969). Sailing ships of the seventeenth and eighteenth century transporting cattle must have provided very favourable conditions for these flies because of low level of hygiene (Hackman, 1969). Thus *C. ferruginata*, *C. hirtula* and *C. vagans* have become cosmopolitan or nearly cosmopolitan (see Table 1.1) while other species, *e.g. Coproica acutangula* (Zetterstedt) and *Coproica hirticula* Collin are spreading rapidly (Papp, 1979a).

Eggs of Sphaeroceridae are white to pale yellowish, elongated ovoid, about three times as long as broad, and usually dorsally flattened (Pitkin, 1989). Larvae are vermiform and have twelve segments. They usually have anterior (prothoracic) and posterior (abdominal) spiracles, which may have numerous finger-like papillae, and the abdominal segments may have ventral rows of short spines or hooks (Pitkin, 1989). The puparium comprises of the sclerotized skin of the third instar larva and, when empty, is translucent white to brown, usually yellowish or golden brown (Pitkin, 1989). In addition, it is more or less an elongated cylindrical structure, tapering at either end and flattened dorsoventrally at the anterior end (Pitkin, 1989).

This study was initiated after the owners of Blokhuis feedlot near Harrismith approached the Department of Zoology and Entomology at the University of the Orange Free State to investigate and control the "midges" that annoyed the cattle. Various attempts by the feedlot owners to control these flies with insecticides were unsuccessful. According to Marshall (1982), Sphaeroceridae have very little direct economic impact in other countries, despite their ubiquity and abundance. However, in South Africa, they constitute a very serious threat to feedlot owners. The feedlots, where cattle are kept in large numbers under artificial conditions, are a relatively new concept in South Africa.

Currently there are 42 feedlots that are affiliated with the Feedlot Association of Southern Africa (see Table 1.2). The number of cattle at each of the feedlots is unknown due to daily fluctuations.

The feedlot industry currently supplies approximately 60% of the total beef production in South Africa, while many farmers have smaller feedlots, but are not affiliated to this association. Shortages are usually supplemented with beef imports from Britain, Australia and neighbouring countries in southern Africa (S.A. Feedlot Association - pers. comm.). Together with the feedlots a number of problems developed. A major one is the presence of flies, including Sphaeroceridae. These flies breed mainly in the wet areas inside the feedlot camps. Although Sphaeroceridae do not feed on blood, they have an irritating effect on the cattle, making the cattle restless and causing stress. Under heavy infestations, the flies form large swarms, often near the feeding-troughs, causing the cattle to avoid the feeding-troughs. A subsequent delay in conditioning the cattle for market often leads to huge financial losses to the feedlot owners. Under extreme conditions of sphaerocerid fly infestation the cattle totally avoided the feeding- troughs by day. By nightfall when fly activity decreased, the hungry animals overfed themselves and consequently drank too much water. This resulted in the occurrence of severe stomach blown-ups and the subsequent death of the animals.

Before experiments on biological or chemical control of the flies could be initiated, certain key questions, regarding the general biology of these two Sphaeroceridae species, needed to be answered. Apparently dung forms the ideal habitat for the Sphaeroceridae, but it is well known that dung lying in the field can undergo rapid changes (Merritt & Anderson, 1977). It was thus important to establish the optimum conditions under which the Sphaeroceridae are able to survive and increase in numbers until they reach the vast number of individuals that become a nuisance to the cattle. Furthermore it was important to determine the reproduction and survival rates of these flies. During this study the following questions were addressed:

(1) How could healthy laboratory colonies be established from flies collected at the feedlots to determine the optimum laboratory conditions that would produce large numbers of flies in a relatively short time (less than three weeks) for further experimental studies in the laboratory?

(2) Why are Sphaeroceridae such a problem at feedlots? Does the composition of feedlot dung differ from that of other dung types? How do different dung types influence the reproduction and survival of the flies?

(3) At certain times of the year under certain conditions, Sphaeroceridae reached high numbers. How many eggs does a single *C. vagans* or *C. hirtula* female lay in these conditions and what is her reproductive period?

(4) Since these flies usually occur during the latter part of summer, to what extent could physical parameters play a role in the abundance of the two species, *C. vagans* and *C. hirtula*, *e.g.* the influence of temperature, moisture and photo-period on oviposition, hatching, development and survival? By testing these parameters on the two species separately, insight could be gained as to why the one species is more dominant at the feedlot than the other.

(5) Which biological or chemical control measures can be introduced to control these flies at the feedlot since little competition for food or space exist at the feedlot for both larvae and adults?

(6) Which areas at the feedlot do the flies affect? - This could mean considerable savings once an integrated control program is in place.

Table 1.2: The 42 feedlots in South Africa affiliated to the South African Feedlot Association.

NAME OF FEEDLOT	DISTRICT
Beefcor	Bronkhorstspruit
Beefmaster	Christiana
Blokhuis Feedlot	Harrismith
Braams Stall Feeding	Durbanville
Chalmer Beef	Bapsfontein
Doringbult Feedlot	Pietersburg
Gysberthoek Feedlot	Sasolburg
Hekpoort Feedlot	Delmas
Hurland Feedlot	Magaliesburg
Ivy Bonsmaras	Tzaneen
JJ Feedlot	Vrede
Kalbasfontein Farming	Witbank
Kanhym LTD	Middelburg, Mpumalanga
Karan Beef	Heidelberg, Gauteng
Kolosus Feedlot	Krugersdorp
Koodoolake Feedlot	Stella
D.C. Louw Farming	Adelaide
M & J Da Costa	Nigel
Majeje Beef	Giyani
Meatco	Windhoek, Namibia
Mollvel Feedlot	Sibasa
Namakor	Delmas
Hartswater Feedlot	Hartswater
Omgesien Feedlot	Alldays
OTK (PTY) LTD	Bethal
Ranch Estates	Delmas
Rooikoppen Feedlot	Standerton
Rustfontein Feedlot	Bronkhortspruit
Sernick (PTY) LTD	Edenville
SKS Farming	Middelburg, Mpumalanga
Simunye Feedlot	Simunye, Swaziland
SIS Farming	Bethal
Sparta Beef	Marquard
Meatbar (PTY) LTD	Naboomspruit
Stock-owners Co-op	Howick
Taaiboschbult Feedlot	Potchefstroom
Tangeni Farming	Dundee
Triple A Beef	Pietermaritzburg
Unico Feedlot	Bethlehem
P.S. Vercuiel Farming	Stella
Vencor Feedlot	Pietersburg
Frotress Bonsmaras	Kempton Park

List updated - June 1997.

CHAPTER 2

SEASONAL OCCURRENCE AND RELATIVE ABUNDANCE OF DOMINANT DIPTERA POPULATIONS USING UNDISTURBED CATTLE DROPPINGS IN THE CENTRAL FREE STATE PROVINCE

2.1 INTRODUCTION

When cattle are kept on pastures and rangeland and are allowed to graze freely, their excrement is scattered about in isolated pats that soon break down and return valuable nutrients to the ecosystem (Poorbaugh, 1966). Numerous, beneficial, coprophagous insect species that are adapted to use the cow pats for larval development and which form a unique community whose members consist mostly of flies are primarily responsible for this breakdown (Poorbaugh *et al.*, 1968). Furthermore, this community of species that inhabit fresh droppings include a few native local species which are able to utilize cattle dung, as well as other types of dung or decaying organic matter for larval growth, although these widely distributed species are generally specific to dung (Poorbaugh, 1966). Merrit (1976) stated that his own and many other faunal studies included lists of dipteran species "reared" from dung. However, this does not necessarily imply that the specific species mentioned feed entirely on dung itself, since larvae may feed on micro-organisms (*e.g.* fungi, bacteria) growing on the dung (Baumberger, 1919), or they are predators or parasitoids.

Cattle droppings provide a special microhabitat for coprophagous organisms. The dynamics of arthropod populations inhabiting dung are influenced by two important factors, environmental conditions in the immediate area in which the pat was dropped and the arthropod community itself (Hammer, 1941; Mohr, 1943). These include their interspecific competition, predator-prey interactions and various processes in their life

histories that may alter the physical or chemical nature of the dung (Hammer, 1941; Mohr, 1943; Valiela, 1974; Merrit & Anderson, 1977).

Studies on the taxonomy, biology and ecology of fauna associated with droppings of pastured cattle have been carried out in Egypt by Hafez (1939), in Denmark by Hammer (1941), in the USA by Mohr (1943) and in Australia by Snowball (1944). In recent years renewed interest was shown in this fauna with specific reference to the fauna inhabiting cattle dung in different geographical areas (Poorbaugh *et al.*, 1968; Blume, 1970, 1972). As was the case in the present study, the majority of succession studies on fauna at or in dung pats were conducted on a seasonal basis, (*e.g.* Laurence, 1954; Poorbaugh, 1966; Papp, 1971 and Merrit & Anderson, 1977).

Literature studies showed no record of surveys that have been done in South Africa and more specifically in the Free State to determine the composition of the Sphaeroceridae population. The primary aim of the current study was to establish which Sphaeroceridae species and other dung-breeding flies are present in cattle dung in the Free State. This study was therefore limited to flies that use cattle dung as a breeding medium, and all other coprophagous dung inhabitants were consequently excluded.

2.2 MATERIAL AND METHODS

2.2.1 Study area

This study was conducted at Hebron (29°6'S;26°1'E), a dairy farm 35 km west of Bloemfontein. The study area was adjacent to a cultivated wheat field and consisted of a small pasture of about two hectares where the vegetation, which consisted mainly of *Themeda triandra* (red grass) and undergrowth, was very sparse (Fig. 2.1). Vegetation sparseness was attributed to the large number of dairy cows that was present in the camp at times and also to the severe drought during the study period. The area was chosen

mainly because of the shady conditions provided by large *Acacia karoo* trees. This made it possible to study the fly fauna in both sunny and shaded conditions. No other large animals with dung suitable for colonization by coprophilic communities occurred in this pasture.

Figure 2.1. Hebron dairy farm, 35 km west of Bloemfontein, Free State, where the fly succession surveys were conducted.

2.2.2 Survey procedure

The study was conducted for eight seasons over a two-year period from January 1992 - December 1993. Each seasonal survey was performed for four consecutive days, in which maximum and minimum air temperatures, as well as other parameters such as wind speed, relative humidity and light intensity were measured throughout the surveys. Rainfall only occurred once during the eight surveys conducted. The temperature inside the dung pat was measured with a thermometer and the humidity inside the dung pats

with a hygrometer. The diameter of the dung pats was also measured during each observational period.

A practical difficulty was encountered during the execution of these surveys. Cattle were not always present in the trial pasture and even when they were, cows did not defecate simultaneously at the study site in the desired manner. Typical defecations were therefore simulated by exposing "artificial" cow pats in the precise time, place and manner desired. This was done by collecting fresh dung at a dairy camp situated about one kilometre from the study area, where a large herd of cows was kept. Fresh dung could be obtained by disturbing cattle that were lying down. If the cows have been resting or ruminating for a time they will defecate upon arising (Poorbaugh, 1966).

Fresh dung was collected in 25-litre plastic buckets and transported to the field site. Care was taken not to contaminate this dung with soil or other detritus from the substrate. To make artificial pats, about two to three litres of dung were formed into a round pat about 7-8 cm thick and 25-30 cm in diameter and re-exposed for faunal attraction and colonization studies. Thirty-two of these artificial pats were placed out at 08:00 on the first day of each survey at the relevant locations. Sixteen of the dung pats were placed under trees in shade while the rest were exposed to the sun. A single pat was re-collected at each of the following intervals; 3 h, 6 h, 9 h, 12 h, 21 h, 24 h, 28 h, 32 h, 45 h, 48 h, 52 h, 56 h, 68 h, 72 h, 76 h and 80 h after starting the experiment. During the night there was no fly activity. Therefore no pats were collected during the night, which explain the time intervals between 12h and 21h; 32h and 45h, as well as between 56h and 68h. During the winter a few of the pats were collected when it was already dark, *e.g.* the 12 h and 21 h intervals, but this was done only to keep the sampling times the same as for the other three seasons. At each of these intervals, two artificial pats were collected, one that was exposed to sun and one from shade. The pats were picked up with a spade and put into large plastic containers, taking care not to break the crust. The containers were then covered with gauze to facilitate ventilation, but also to exclude flies that were not

associated with the experiment. All the pats were transferred to the laboratory and kept in a temperature controlled room set at 24 ± 1°C until faunal emergence was completed. Because most dung pats in the field were damaged by predators after 80 hours, it was decided not collected any pats beyond this period.

2.2.3 Collection and identification of fly species

After one week, the first adult flies started to emerge and they were collected into a plastic container that was mounted on a suction apparatus. This was done on a daily basis. Flies were killed by spraying them with 70% ethanol, taking care that none of the flies escaped. They were then counted and sent to Mr. A.E. Whittington for identification.

Unfortunately only some of the identifications were done to genus or species level, especially the Sepsidae and Muscidae, because no up-to-date keys exist for these families and therefore identifications had to be treated with extreme caution (Mr. A.E. Whittington, pers. comm.). [*Orthelia perronii* Robineau-Desvoidy (Muscidae) was identified by Mr. E.J. Leipoldt].

Initially several attempts were made to identify the five Sphaeroceridae species collected. At first a key for Sphaeroceridae supplied by Pitkin (1989) was used. This proved to be unsuccessful because it was a key only to British Sphaeroceridae. These specimens were then send to two Dipterologists, Pitkin and Rohacèk, who specialize in Sphaeroceridae. Both mentioned that all five specimens were probably undescribed species and the species were only identified to subfamily level. No *C. vagans* or *C. hirtula* species were found during these succession studies, which indicate that these two species probably do not colonize isolated dung pats in the field or have not yet spread to the Hebron area.

The succession experiments only involved the rearing of flies that developed and completed their entire life cycle in the dung. Since organisms such as spiders, mites, certain fly species and other arthropods that visited the pats for shelter or only to feed on the fluid from the droppings were not sampled by the methods used in this study, they were not evaluated. Since only Diptera were emphasized in this investigation, no attempt was made to provide a complete listing of the Coleoptera community. The Coleoptera community in dung was investigated by Geyser (1994).

2.3 RESULTS AND DISCUSSION

2.3.1 Faunal analysis

Twenty-one Diptera species emerged from artificially exposed droppings that were brought to the laboratory after exposure in the field for between 3 and 80 hours. In Table 2.1, the different Diptera species inhabiting or colonizing droppings at Hebron during the four seasons are arranged in family groups. In all instances families have been retained as a distinct entity (*e.g.* Sphaeroceridae, Sepsidae, Muscidae).

This survey essentially involved the rearing of Diptera from dung samples where it was presumed that the emergence counts of adults of the various species reflected their abundance at the time of colonization. This is not always the most accurate method, because Poorbaugh (1966) stated that mortality of immature stages within individual droppings could be expected to vary depending upon the number of predators and prey species that originally colonized the pat. He also suggested several ways in which succession studies could be conducted, which included visual counts, larval extraction, as well as identification and collection of flies from the pats by means of an insect sweeping net (Poorbaugh, 1966). However, the small size of some flies, such as the Sphaeroceridae, enabled them to move into minute cracks within or underneath dung pats, and because of their sluggish behaviour, they are not readily disturbed. This made

visual counting and collection of these small flies with an insect net impossible. Larval extraction was not considered because it would have been extremely difficult to identify the larvae to species level. Rearing flies from undisturbed droppings was therefore the best option. In his studies Poorbaugh (1966) showed that emergence patterns of the various species from pats lying about the pastures generally reflected colonization patterns accurately. However, in the USA, Poorbaugh (1966) also found that of the 68 species of Diptera that were attracted to dung, only 47 were reared from the droppings because some of the attracted species only fed on dung and also obtained moisture from it during drier seasons. Therefore, during dry seasons, fresh cattle dung may be an important factor in the ecology of many insects. These findings by Poorbaugh also highlighted one of the shortcomings of this particular sampling method. This could imply that many more fly species (besides the 21 species that were reared from the dung) visited the pats only to feed on the liquid content of the dung.

Table 2.1: Diptera fauna associated with fresh cattle dung collected at Hebron during four seasons of 1992 and 1993.

SPHAEROCERIDAE	Limosininae sp. 1
	Limosininae sp. 2
	Limosininae sp. 3
	Limosininae sp. 4
	Sphaerocerinae sp
SEPSIDAE	*Sepsis thoracica* (Robineau-Desvoidy)
	Sepsis sp. 1
	Sepsis sp. 2
	Nemopoda sp. 1
	Nemopoda sp. 2
MUSCIDAE	*Musca* (*Eumusca*) *xanthomelas* Wiedemann
	Musca (*Philaematomyia*) *crassirostris* Stein
	Phaonia sp. 1
	Phaonia sp. 2
	Muscinae sp. 1
	Muscinae sp. 2
	Orthelia perronii (Robineau-Desvoidy)
	Orthelia nudissima (Loew)
	Musca sp. 1
	Musca sp. 2
SARCOPHAGIDAE	*Sarcophaga cruentata* Meigen

2.3.2 Individual differences between different seasons

The largest total number of individuals (all families included) collected during a season was 18275 and this was recorded from the shaded pats during summer (Fig. 2.2). However, a large number of individuals were also collected from shaded pats during spring (Fig. 2.2). During the colder autumn and winter seasons, fly abundance gradually decreased with the onset of lower temperatures. The total number of individuals per season was as low as 399 and this was recorded at shaded pats in winter. On sunny pats in winter a total of 505 individuals were collected (Fig. 2.2).

The nature of a succession depends on seasonal variation as far as the numbers of individuals of the different species are concerned. Factors such as temperature, rainfall, wind, sunshine and relative humidity greatly affect the duration of visits by most fly species (Mohr, 1943). The mean temperatures and relative humidities recorded during the individual surveys were measured and are presented in Figure 2.3. A clear trend can be seen as far as temperature is concerned. During the summer when environmental temperatures were high during the day and night, the success rate of rearing flies from undisturbed droppings in the field was higher compared to the other three seasons (see Table 2.2). This demonstrated the importance of favourable temperatures in and around the pats to ensure a higher success rate in terms of the immature fly development and adult survival. During summer and spring when temperatures were higher, more flies were collected from shaded dung pats, while during cooler seasons such as autumn and winter, the number of flies that were collected from sunny pats were higher (Fig. 2.2).

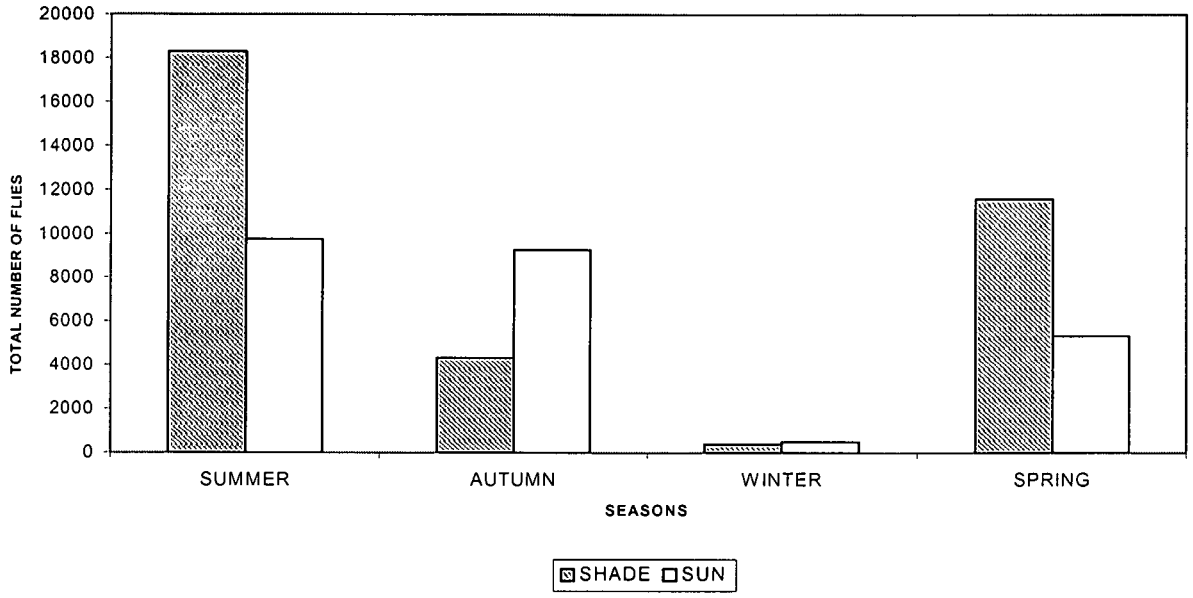


Figure 2.2. The total number of individuals (all families included) recorded from shaded and sunny dung pats during each of the four seasons in 1992 and 1993.

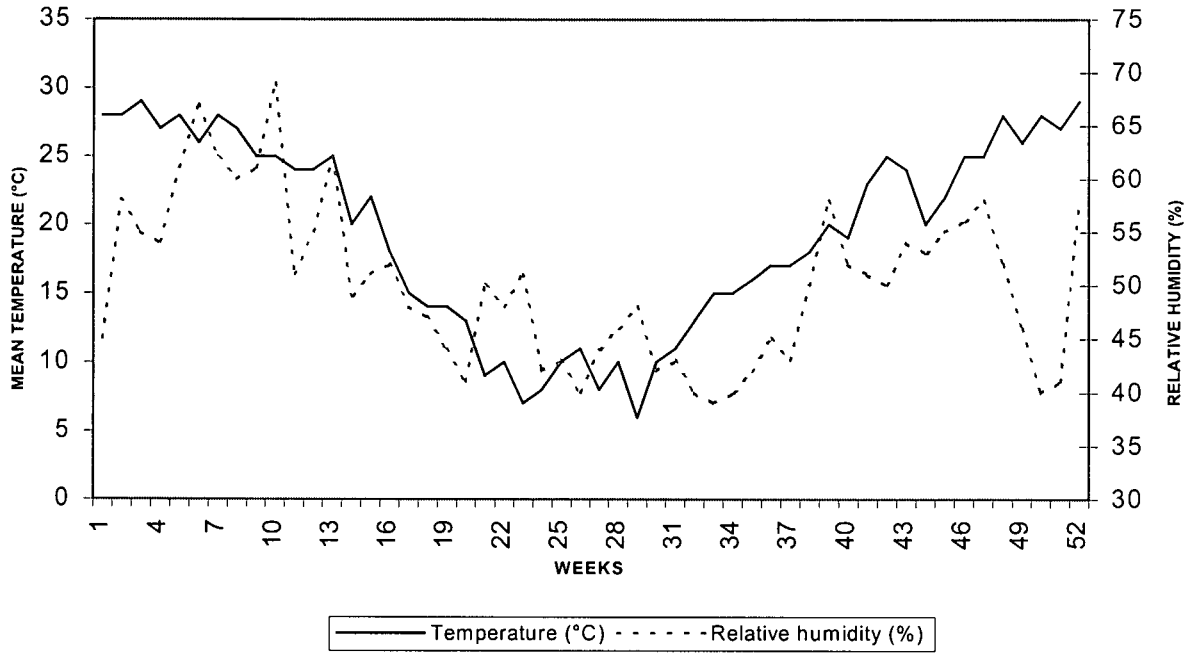


Figure 2.3: The mean temperatures and relative humidities recorded during 1992 and 1993. (Data obtained from the weather bureau in Bloemfontein).

However, this same trend is not as clearly defined when relative humidity is considered (Fig. 2.3). Although differences in relative humidities during summer and spring could be seen, more flies were collected during summer, probably owing to more favourable temperature conditions (Figs 2.2 & 2.3). During autumn for instance, the relative humidity was very similar compared to the relative humidities in spring, and yet more flies were collected during autumn. It is probable that most of the attracted species feed on dung as well as obtaining moisture from it during the dry and hotter season. In fact, during the dry season, fresh cattle dung may be an important factor in the ecology of many insects (Laurence, 1954), especially in the Central Free State where very little rain usually falls from late autumn to early spring. Moisture was therefore undoubtedly an important factor in these succession studies because it is known that dung-breeding flies are attracted to moist dung for both nourishment and breeding. Hammer (1941) also emphasized that water content of manure could become a limiting factor to larvae of face flies (*Musca autumnalis* De Geer) if the dung became too dry to allow feeding. Laurence (1955) found that adults of the sphaerocerid *C. scutellaris* were attracted to moist dung. In summer, this species had been reared mainly from shaded pats, where dung moisture was retained for longer periods and a distinct crust did not form as quickly. However, *C. lugubris,* a species that occurred abundantly in pats in full sunshine, had not been attracted to shaded pats (Laurence, 1955). It therefore seems as if a combination of all factors such as temperature, relative humidity and light intensity were responsible for creating optimum conditions, which then played a role in determining fly populations. This is also the view of Engroff *et al.* (1972) who concluded that many factors in combination, such as temperature, relative humidity and wind speed, contributed to fly activity in a complex way.

Although it became apparent that temperature and relative humidity were important factors in determining the abundance of flies on dung pats in the field, it seemed as if light intensity was also important because more flies were collected from shaded pats during the warmer seasons. However, this phenomenon could also be attributed to the

effect of temperature, since conditions in the shade during winter and in the sun during summer were probably too unfavourable for many of the adult flies. This also concurs with findings by Hammer (1941), who stated that most flies had a period of activity that began in the morning when temperatures had risen above the lowest limit of their activity and when the intensity of light had reached a suitable degree. It therefore seems that in the present study, a combination of temperature and light intensity should be considered in explaining fly abundance on certain dung pats during the different seasons. Hammer (1941) also stated that light and temperature were the most influential factors on face fly activity because they had a peak of abundance at midday during the warm summer period and had disappeared from dung pats in the evening owing to their relation to light. He furthermore noted that some species, *e.g. Haematobia irritans* (Linnaeus) occurred on pats when temperatures ranged from 10°C to 17°C, but it was presumably the light intensity that was of greatest importance, because neither air temperature nor relative humidity seemed to be determining factors in this case (Hammer, 1941). Treece (1960) also indicated that more face flies settled on cattle on bright sunny days than on darker overcast days.

2.3.3 Seasonal occurrence and relative abundance of predominant coprophilic flies in the field

Particularly large numbers of Sphaeroceridae were collected from single shaded dung pats during summer and spring, while in autumn and winter the majority of sphaerocerids were collected from single sunny pats (Table 2.2). A peak number of 1073 flies were collected from an individual sunny pat in autumn, while a peak number of 825 also emerged from an individual shaded pat during spring (Table 2.2). However, during the winter, small numbers of Sphaeroceridae emerged from both sunny and shaded dung pats (Table 2.2).

Table 2.2: Peak numbers of flies collected of each family from a single sunny and shaded dung pat during four seasons. The times where these peak numbers were reached are shown in brackets (compare with Tables 2.4 – 2.11).

	Summer		Autumn		Winter		Spring	
	shade	sun	shade	sun	shade	sun	shade	sun
Sphaeroceridae	1319 [12h]	371 [28h]	261 [21h]	1073 [9h]	18 [48h]	48 [72h]	825 [28h]	45 [6h]
Sepsidae	758 [12h]	1421 [12h]	505 [12h]	396 [9h]	154 [72h]	25 [68h]	399 [24h]	414 [9h]
Muscidae	656 [9h]	25 [3h]	95 [32h]	50 [48h]	3 [48h]	16 [76h]	521 [24h]	308 [32h]
Sarcophagidae	17 [9h]	6 [9h;72h]	0	0	0	2 [52h]	0	6 [21h]

Sphaeroceridae usually represented between 3% and 85% of all flies collected from the dung (Table 2.3). However, they were not well represented on dung collected from sunny pats in spring, because only 3% were Sphaeroceridae, while 85% of flies collected from dung pats at sunny locations during autumn were Sphaeroceridae (Table 2.3).

Sepsidae were abundant during all four seasons, especially during summer, where a peak of 1421 sepsid flies were collected from the sunny pats and a peak of 758 from the shaded ones (Table 2.2). During autumn a peak of 505 and 396 sepsids were reared from both shaded and sunny pats respectively, while in spring peak numbers of 399 and 414 flies were reared from shaded and sunny pats respectively. Their numbers during winter were as low as 25 on sunny pats (Table 2.2).

Sepsidae usually represented a large percentage of the total number of flies that were reared from the dung pats, with the exception of sunny pats in autumn where only 13% of the flies collected were Sepsidae (Table 2.3). Although a large number of Sepsidae were recorded during the summer as mentioned above, they represented only 19% of the

total number of flies collected from the shaded pats, while 61% of the flies collected from the sunny pats during summer were Sepsidae (Table 2.3).

Table 2.3. Seasonal occurrence of dominant Diptera families on single shaded and sunny pats collected over an 80-hour-period, represented as a percentage of the total number of flies collected.

	Summer		Autumn		Winter		Spring	
	shade	sun	shade	sun	shade	sun	shade	sun
Sphaeroceridae	57	37	57	85	8	47	38	3
Sepsidae	19	61	34	13	90	33	37	64
Muscidae	23	1	9	2	2	19	25	32
Sarcophagidae	1	1	-	-	-	1	-	1

In comparing the seasonal abundance of Sphaeroceridae and Sepsidae with each other, a degree of ecological displacement could be observed from Table 2.3. This effect was especially obvious on all shaded and sunny pats during all four seasons, except on shaded pats in spring. At times when Sphaeroceridae represented a large percentage of the total number of flies collected, Sepsidae represented a much smaller percentage and vice versa. An example of this effect could be seen on shaded pats in winter, where 90% of the flies collected were Sepsidae and only 8% Sphaeroceridae, while on sunny pats in autumn 85% of the total number of flies collected were Sphaeroceridae and only 13% Sepsidae (Table 2.3).

The number of Muscidae collected from all dung pats was sometimes very low in comparison to the other two families. The only exceptions were on shaded pats in summer and both shaded and sunny pats in spring, where relatively large numbers were collected where peak numbers ranged between 308 and 656 flies per pat (Table 2.2). However, it is important to keep in mind that muscids are generally larger in size and

have larger larvae than Sphaeroceridae and Sepsidae, and fewer muscids could be expected from each individual dung pat. According to Table 2.3, between 9% and 32% of flies collected from both sunny and shaded pats were Muscidae. The only exceptions were during autumn and summer (sunny pats only) and on shaded pats in winter, where only between1% and 2% of the flies were Muscidae.

The diversity and relative abundance of the predominant fly species breeding in sunny and shaded dung pats are shown in Tables 2.4 - 2.11. Data is only for families that completed their life cycles in the dung. Fly faunal composition of droppings during all four seasons comprised three families, Sphaeroceridae, Sepsidae and Muscidae. One other family, Sarcophagidae, only emerged in small numbers and only one species, *S. cruentata* was encountered.

The **Sphaeroceridae** was of particular interest, but unfortunately only five sphaerocerid species were collected from all dung pats. Four species were identified as species of the subfamily Limosininae and one of Sphaerocerinae (Table 2.1). There could have been more species, because Rohacèk (1983) stated that excrement serves as a feeding substrate for both larvae and adult Sphaeroceridae. Therefore it is important to stress that some species may have occurred only as adults on droppings, whilst developing in other organic matter. Rohacèk (1983) found that many species of this large family of small, grey-black flies occurred in pats throughout the year, and most of the time several species emerged from the same pat. These flies were among the first to visit the fresh droppings because large numbers were collected from dung pats that were exposed for only three hours (Tables 2.4 - 2.11). Laurence (1955) referred to these fly species which arrive first at the newly formed droppings as the "primary inhabitants" of dung.

Table 2.4: Succession of flies reared from cow pats in the shade over an 80-hour-period during summer.

Time in hours -	3	6	9	12	21	24	28	32	44	48	52	56	68	72	76	80	TOTAL
SPHAEROCERIDAE																	
Limosininae sp1	510	428	491	1281	816	912	774	711	612	643	510	311	303	209	210	68	8789
Limosininae sp2		12	19	17	38	102	8	178	49	11	18	52	68	34	57	22	685
Limosininae sp3	2	2	19	8	17	52	41	99	97	22	19	21	40	5	33	6	483
Limosininae sp4				1			4	35		3	4						47
Sphaerocerinae sp	4	5	8	12	2	70	113	48	213	78	15	8	2	12	13	16	619
TOTAL	516	447	537	*1319	873	1136	940	1071	971	757	566	392	413	260	313	112	10623
SEPSIDAE																	
Sepsis thoracica	191	119	335	336	138	118	120	65	152	148	105	91	41	43	51	37	2090
Sepsis sp1	23	21	47	32	18	2	7	4	11	3	2			3	3	7	183
Sepsis sp2			1	3		2	5										11
Nemapoda sp1	86	25	195	281	39	54	48	10	13	16	12	30	9	11	24	1	854
Nemapoda sp2	31	13	22	106	19	11	13	13	6	15	9	6	15	3	60	3	345
TOTAL	331	178	600	*758	214	187	193	92	182	182	128	127	65	60	138	48	3483
MUSCIDAE																	
Musca xanthomelas	1	1	1	3	4	5	14		4		3	2	24	1	6	3	72
Musca crassirostris	2	11	13	1		1		9	2	3						1	43
Phaonia sp1				1						1				1		1	4
Phaonia sp2					1					1							2
Muscinae sp1		2	2	6	7	2	1	3					1		4		28
Muscinae sp2	1	6		9	3			1					7	4	1		32
Orthelia perronii	629	418	640	157	9	426	170	6	211	244	208	203	132	323	31	147	3954
Orthelia nudissima		1		1													
Musca sp1																	
Musca sp2																	
TOTAL	633	439	*656	178	24	434	185	19	217	249	211	205	164	329	42	152	4137
SARCOPHAGIDAE																	
Sarcophaga cruentata	6		*17		1			1							7		32
Note: [*] indicates peak numbers																	18275

Table 2.5: Succession of flies reared from cow pats in the sun over an 80-hour-period during summer.

Time in hours -	3	6	9	12	21	24	28	32	44	48	52	56	68	72	76	80	TOTAL
SPHAEROCERIDAE																	
Limosininae sp1	212	118	281	155	212	306	288	219	144	141	79	104	81	55		12	2407
Limosininae sp2	1	2	30	76	61	23	48	45	125	69	52	37	39	4	7	18	637
Limosininae sp3		5	14	77	25	37	25	36	64	42	70	52	18	40	35	20	560
Limosininae sp4	8									10							18
Sphaerocerinae sp				21	1	2	10			2	4						40
TOTAL	221	125	325	329	299	368	*371	300	333	264	205	193	138	99	42	50	3662
SEPSIDAE																	
Sepsis thoracica	183	148	146	820	212	319	30	215	324	611	670	209	28	29	29	3	3976
Sepsis sp1	32	13	13	77	10	36	1	2	9	5	5	2	8	2	5		220
Sepsis sp2																	
Nemapoda sp1	136	117	104	524	143	72	45	38	81	194	224	48	5	9	2	4	1746
Nemapoda sp2																	
TOTAL	351	278	263	*1421	365	427	76	255	414	810	899	259	41	40	36	7	5942
MUSCIDAE																	
Musca xanthomelas	19	1	5	1	12		2	3		2		3	1		4	1	54
Musca crassirostris																	
Phaonia sp1																	
Phaonia sp2																	
Muscinae sp1	4			5	4	5	1		1		1		4		3		28
Muscinae sp2	2			9	2	5	11	1	1		1		3				35
Orthelia perronii																	
Orthelia nudissima		1		1													2
Musca sp1																	
Musca sp2																	
TOTAL	*25	2	5	16	18	10	14	4	2	2	2	3	8		7	1	119
SARCOPHAGIDAE																	
Sarcophaga cruentata			6					5							6		17
Note: [*] indicates peak numbers																	9740

Table 2.6: Succession of flies reared from cow pats in the shade over an 80-hour-period during autumn.

Time in hours -	3	6	9	12	21	24	28	32	44	48	52	56	68	72	76	80	TOTAL
SPHAEROCERIDAE																	
Limosininae sp1			118	182	192	202	171	97	138	201	241	91	188	184	77	81	2163
Limosininae sp2			2	29	52	21	33	14	19	22	1	14	17	2	2		228
Limosininae sp3		1	1	3	17	18		1		3	1			1			46
Limosininae sp4																	
Sphaerocerinae sp			2	3		1	1										7
TOTAL		1	123	217	*261	242	205	112	157	226	243	105	205	187	79	81	2444
SEPSIDAE																	
Sepsis thoracica	18	101	177	172	25	15	3			3	12						526
Sepsis sp1	4	28	33	48	1	2											116
Sepsis sp2																	
Nemapoda sp1		63	145	285	119	92	61	15	39		2	13	21	10	3		868
Nemapoda sp2																	
TOTAL	22	192	355	*505	145	109	64	15	39	3	14	13	21	10	3		1510
MUSCIDAE																	
Musca xanthomelas										1		1					2
Musca crassirostris					1												1
Phaonia sp1																	
Phaonia sp2																	
Muscinae sp1			1				1			3							5
Muscinae sp2						3		2		1		3	2	1		2	14
Orthelia perronii		1		12	13	20	81	92	43	17	28	33	4	8	14	2	368
Orthelia nudissima																	
Musca sp1	1			1	1	1					1			2		1	8
Musca sp2						1		1									2
TOTAL	1	1	1	13	15	25	82	*95	43	22	29	37	6	11	14	5	400
SARCOPHAGIDAE																	
Sarcophaga cruentata																	0
Note: [*] indicates peak numbers																	4354

Table 2.7: Succession of flies reared from cow pats in the sun over an 80-hour-period during autumn.

Time in hours -	3	6	9	12	21	24	28	32	44	48	52	56	68	72	76	80	TOTAL
SPHAEROCERIDAE																	
Limosininae sp1		66	1012	881	512	681	612	518	505	381	356	409	551	412	400	316	7612
Limosininae sp2	1			17		1	17	2	18	41	16	14	17	2	2		148
Limosininae sp3				2							5	4		2			13
Limosininae sp4				5	6												11
Sphaerocerinae sp		48	61	14	5	2											130
TOTAL	1	114	*1073	919	523	684	629	520	523	422	377	427	568	416	402	316	7914
SEPSIDAE																	
Sepsis thoracica		72	218	202		2	16	56	71	88	16	15	2	3		5	766
Sepsis sp1		17		1	1	1											20
Sepsis sp2																	
Nemapoda sp1	2	161	178	16		16	13		16	19			5			1	427
Nemapoda sp2																	
TOTAL	2	250	*396	219	1	19	29	56	87	107	16	15	7	3		6	1213
MUSCIDAE																	
Musca xanthomelas		1	3		1	1				2							8
Musca crassirostris																	
Phaonia sp1																	
Phaonia sp2																	
Muscinae sp1	2	3	18			12	3	11	13	48		5		3			118
Muscinae sp2				2	1	4		3			1				1		12
Orthelia perronii																	
Orthelia nudissima																	
Musca sp1		2		1		1									1	1	6
Musca sp2			1	2		1		1			1		1				7
TOTAL	2	6	22	5	2	19	3	15	13	*50	2	5	1	3	2	1	151
SARCOPHAGIDAE																	
Sarcophaga cruentata																	0
Note: [*] indicates peak numbers																	9278

Table 2.8: Succession of flies reared from cow pats in the shade over an 80-hour-period during winter.

Time in hours -	3	6	9	12	21	24	28	32	44	48	52	56	68	72	76	80	TOTAL
SPHAEROCERIDAE																	
Limosininae sp1																	
Limosininae sp2		2						3		15							20
Limosininae sp3			5					1		3						1	10
Limosininae sp4																	
Sphaerocerinae sp																	
TOTAL		2	5					4		*18						1	30
SEPSIDAE																	
Sepsis thoracica		15	42	13			16	6		11		5		62		15	185
Sepsis sp1									2	11		3		51			67
Sepsis sp2																	
Nemapoda sp1		7	8		2		3		2	3	23	12	6	41		2	109
Nemapoda sp2																	
TOTAL		22	50	13	2		19	6	4	25	23	20	6	*154		17	361
MUSCIDAE																	
Musca xanthomelas								2		3					1		6
Musca crassirostris																	
Phaonia sp1			2														2
Phaonia sp2																	
Muscinae sp1																	
Muscinae sp2																	
Orthelia perronii																	
Orthelia nudissima																	
Musca sp1																	
Musca sp2																	
TOTAL			2					2		*3					1		8
SARCOPHAGIDAE																	
Sarcophaga cruentata																	0
Note: [*] indicates peak numbers																	399

Table 2.9: Succession of flies reared from cow pats in the sun over an 80-hour-period during winter.

Time in hours -	3	6	9	12	21	24	28	32	44	48	52	56	68	72	76	80	TOTAL
SPHAEROCERIDAE																	
Limosininae sp1	13	15			18	12	25			17	33		12	48		17	210
Limosininae sp2			1	1		4						1					7
Limosininae sp3			2		3		1			5	2	2	2			1	18
Limosininae sp4																	
Sphaerocerinae sp																	
TOTAL	13	15	3	1	21	16	26			22	35	3	14	*48		18	235
SEPSIDAE																	
Sepsis thoracica	12	15	17	6	12	11	17		6	17	8	19	25			2	167
Sepsis sp1																	
Sepsis sp2																	
Nemapoda sp1																2	2
Nemapoda sp2																	
TOTAL	12	15	17	6	12	11	17		6	17	8	19	*25			4	169
MUSCIDAE																	
Musca xanthomelas	3	2		1	2	2	1		1			4	9	1	8	1	35
Musca crassirostris																	
Phaonia sp1																	
Phaonia sp2																	
Muscinae sp1	1	2		1	8	6	1	4		3				2	4	1	33
Muscinae sp2	2			4	1	7	2		1	3	2		1		4		27
Orthelia perronii																	
Orthelia nudissima																	
Musca sp1																	
Musca sp2																	
TOTAL	6	4		6	11	15	4	4	2	6	2	4	10	3	*16	2	95
SARCOPHAGIDAE																	
Sarcophaga cruentata			1				1		1		2				1		6
Note: [*] indicates peak numbers																	505

Table 2.10: Succession of flies reared from cow pats in the shade over an 80-hour-period during spring.

Time in hours -	3	6	9	12	21	24	28	32	44	48	52	56	68	72	76	80	TOTAL
SPHAEROCERIDAE																	
Limosininae sp1	108	151	106	291	80	183	118	125	109	82	71	66	214	214	182	72	2172
Limosininae sp2					2	5			11	16		2					36
Limosininae sp3					1		2		2				1	1		1	8
Limosininae sp4																	
Sphaerocerinae sp	12	2	51	17	33	115	705	275	105	502	310	72	1	18	8	13	2239
TOTAL	120	153	157	308	116	303	*825	400	227	600	381	140	216	233	190	86	4455
SEPSIDAE																	
Sepsis thoracica	302	248	191	121	218	351	255	52	240	298	251	176	175	125	118	77	3198
Sepsis sp1	16		7	2				3		15	18			5			66
Sepsis sp2																	
Nemapoda sp1	27	32	135	115	13	7	23		5	16	5			3	30	18	429
Nemapoda sp2	43	80	18	81	34	41	27	49	74	25	45	39	13	9	9	1	588
TOTAL	388	360	351	319	265	*399	305	104	319	354	319	215	188	142	157	96	4281
MUSCIDAE																	
Musca xanthomelas	4						3										7
Musca crassirostris																	
Phaonia sp1																	
Phaonia sp2																	
Muscinae sp1				5	4					6	1	1					17
Muscinae sp2	2	1		12	5	3	1					1					25
Orthelia perronii		104	190	205	195	518	248	253	200	130	51	210	108	211	81	105	2809
Orthelia nudissima																	
Musca sp1																	
Musca sp2																	
TOTAL	6	105	190	222	204	*521	252	253	200	136	52	212	108	211	81	105	2858
SARCOPHAGIDAE																	
Sarcophaga cruentata																	0
Note: [*] indicates peak numbers																	11594

Table 2.11: Succession of flies reared from cow pats in the sun over an 80-hour-period during spring.

Time in hours -	3	6	9	12	21	24	28	32	44	48	52	56	68	72	76	80	TOTAL
SPHAEROCERIDAE																	
Limosininae sp1																	
Limosininae sp2		45	2	18	3	15	36	13		3	12						147
Limosininae sp3								2		2				2		3	9
Limosininae sp4																	
Sphaerocerinae sp																	
TOTAL		*45	2	18	3	15	36	15		5	12			2		3	156
SEPSIDAE																	
Sepsis thoracica	3	61	301	178	106	188	164	81	204	171	115	166	140	61	51	13	2003
Sepsis sp1	2	40	88	150	195	116	75	16	51	91	15	35	61	8	16	3	962
Sepsis sp2																	
Nemapoda sp1	2	19	25	35	91	86	66	28	23	18	52	13	18	28	8	5	517
Nemapoda sp2																	
TOTAL	7	120	*414	363	392	390	305	125	278	280	182	241	219	97	75	21	3482
MUSCIDAE																	
Musca xanthomelas				1								1					2
Musca crassirostris																	
Phaonia sp1			1		5	2		3									11
Phaonia sp2																	
Muscinae sp1		2		5	2	4		1	2	1		1		1	3		22
Muscinae sp2				6				1					1	2			10
Orthelia perronii	15	124	215	171	13	68	18	301	246	116	8	51	14	245	18	8	1631
Orthelia nudissima																	
Musca sp1				1		1		2	12		1	1			1		19
Musca sp2		2		1	1	4				1							9
TOTAL	15	128	216	185	21	79	18	*308	260	118	9	54	15	248	22	8	1704
SARCOPHAGIDAE																	
Sarcophaga cruentata					6												6
Note: [*] indicates peak numbers																	5348

Limosininae sp. 1

Limosininae sp. 1 is an extremely small sphaerocerid (less than 0.7 mm in length) that occurred in large numbers on the dung (up to 1281 per pat), especially during summer (Table 2.4). They were usually among the first Sphaeroceridae to appear on the fresh droppings. More emerged from shaded pats than sunny pats (compare Figs 2.4 & 2.5). However, their numbers declined on shaded during spring (Fig. 2.4D). In spite of their smaller size, they were the predominant sphaerocerid species on shaded dung pats in summer and autumn, where they represented between 83% (Fig. 2.4A) and 88% (Fig. 2.4B) of all Sphaeroceridae collected, as well as on sunny pats in autumn (Fig. 2.5B) and winter (Fig. 2.5C). They were absent from shaded pats in winter (Fig. 2.4C) and from sunny pats during spring (Fig. 2.5D).

Limosininae sp. 1 reached peak numbers of abundance (1281) at 12 hours in the shade during summer (Table 2.4) and after 24 hours in the sun (Table 2.5). During autumn, they reached peak numbers at 52 hours in the shade pats (Table 2.6) and at 9 hours in the sun (Table 2.7), while in winter, they only occurred periodically and then in small numbers on sunny pats only (Table 2.9). In spring this species was only collected from shaded pats where peak numbers were recorded at 12 hours. However, large numbers were also collected from shaded pats between 52 and 72 hours (Table 2.10).

Limosininae sp. 2

Limosininae sp. 2 is light brown to yellowish in colour and is a much larger sphaerocerid than the first species (approximately 1.5 - 1.8 mm in length). Limosininae sp. 2 was present during all four seasons, but was particularly abundant (up to 178 per pat) on shaded pats in summer (Table 2.4). During spring, they were the predominant Sphaeroceridae species collected from dung pats in the sun where they comprised 94% of all Sphaeroceridae collected (Fig. 2.5D). On the shaded pats in winter, fewer

individuals were found, but they still represented 67% of the total number of Sphaeroceridae collected (Fig. 2.4C). In all other cases only between 1% and 17% of all Sphaeroceridae that were reared from the dung pats were Limosininae sp. 2.

In summer, Limosininae sp. 2 reached peak numbers after dung was exposed in the field for 32 hours on shaded pats (Table 2.4) and after 44 hours on sunny pats (Table 2.5), while peak numbers were reached at 21 and 48 hours during autumn on shaded and sunny pats respectively (Tables 2.6 & 2.7). Very few individuals on a few of the shaded and sunny pats were collected during winter. The largest number sampled was 15 that occurred on the shaded pats at 48 hours (Table 2.8). During spring their numbers increased again and peak numbers were reported at 6 and 48 hours on the sunny and shaded pats respectively (Tables 2.10 & 2.11).

Limosininae sp. 3

Limosininae sp. 3 is a fairly large blackish sphaerocerid that represented between 1% and 33% of the Sphaeroceridae population collected from dung pats (Figs 2.4 & 2.5). Although their numbers were generally low, they represented a large percentage of sphaerocerids collected from shaded pats in summer and winter (15% and 33% respectively) (Fig. 2.4A & 2.4C). They usually only represented between 1% and 8% of all the sphaerocerid species that were collected (Figs. 2.4 & 2.5).

Limosininae sp. 3 reached peak numbers after an exposure period of 32 hours on shaded pats (Table 2.4) and after 12 hours on sunny pats (Table 2.5) in summer. During autumn their numbers dropped, although peak numbers were distinguishable at 21 and 24 hours on the shaded pats (Table 2.6). Very few individuals were collected from sunny pats in autumn (Table 2.7) and then from only a few of the dung pats. This was also the case during winter and spring on both shaded and sunny droppings (Tables 2.8 - 2.11).

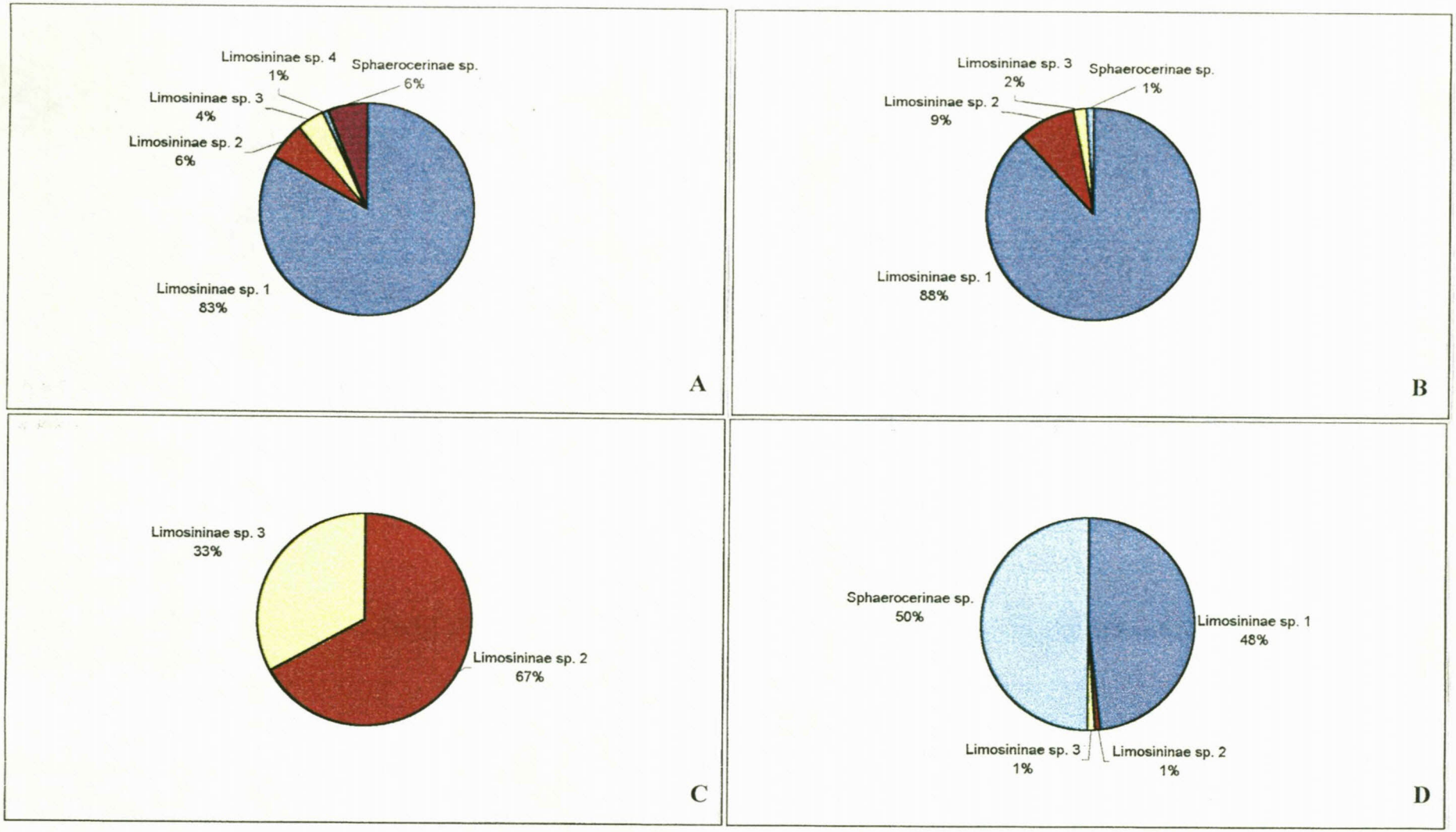


Figure 2.4: Species composition of Sphaeroceridae collected from dung pats in the shade during four different seasons of 1992 and 1993. (Key: A – Summer; B – Autumn; C- Winter; D – Spring).

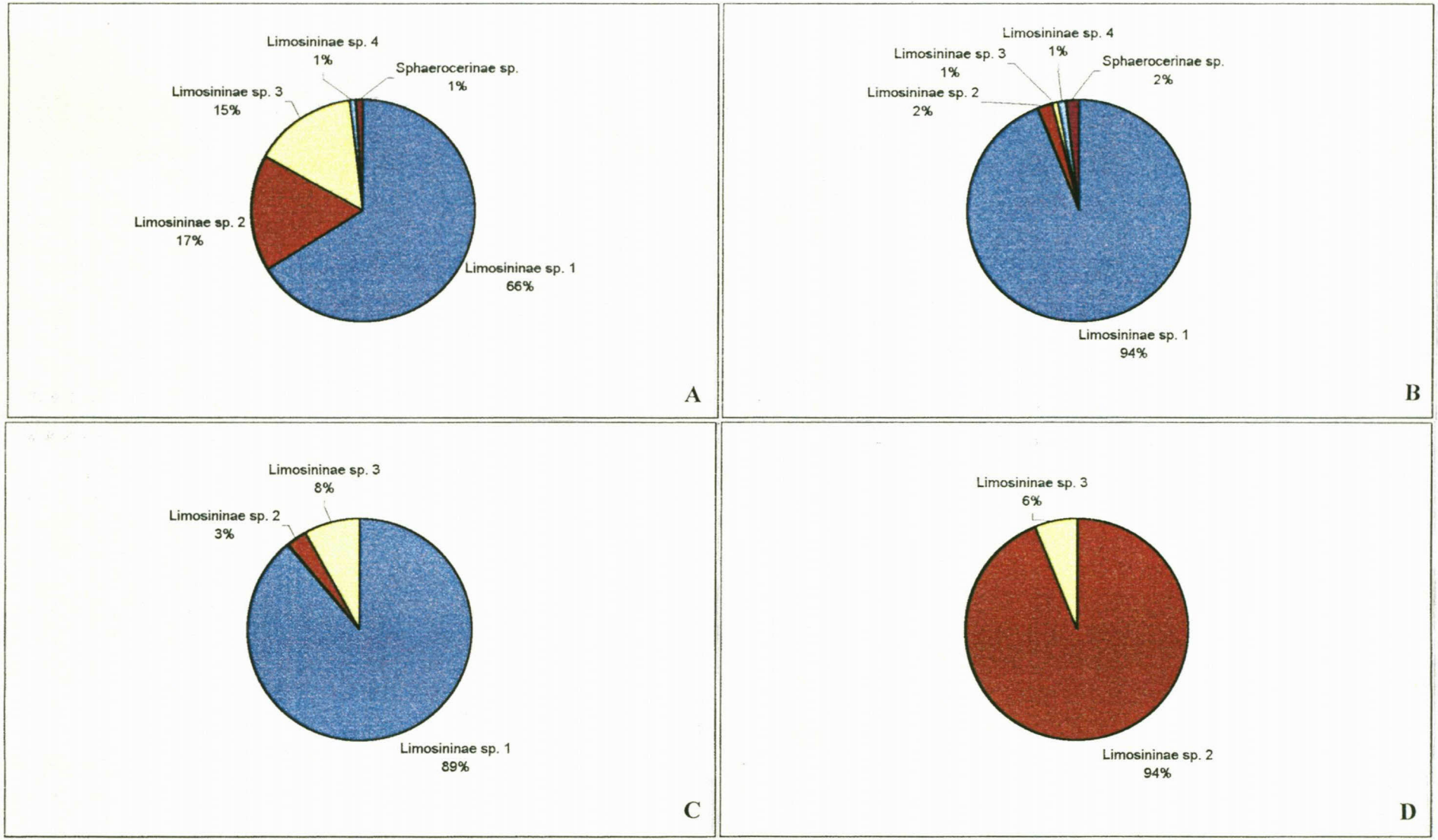


Figure 2.5: Species composition of Sphaeroceridae collected from dung pats in the sun during four different seasons of 1992 and 1993. (Key: A – Summer; B – Autumn; C- Winter; D – Spring).

Limosininae sp. 4

Limosininae sp. 4 is an easy recognizable dark brown species that is up to 2 mm in length. Their movement on the dung pats was more sluggish compared to the other four sphaerocerid species. Limosininae sp. 4 only occurred in small numbers on a few shaded (Table 2.4) and sunny dung pats (Table 2.5) in summer. They also occurred on sunny pats in autumn (Table 2.7). In all three cases only 1% of the total number of Sphaeroceridae that were reared was Limosininae sp. 4. They were not only absent from shaded pats in autumn, but also during winter and spring.

On the shaded pats in summer, peak numbers (35) were collected at the 32 hour interval, although their occurrence was generally sporadic and they were only sampled from five of the dung pats (Table 2.4). They were not considered as early visitors to the droppings - the only time they were sampled from a 3-hour old dung pat was in summer on sunny dung pats.

Sphaerocerinae sp.

Sphaerocerinae sp. was the largest sphaerocerid collected (approximately 3.5 mm in length) and has a light brownish colour. They were present mainly on shaded pats during spring (up to 705 individuals per pat) (Table 2.10). They also occurred during summer and autumn on both sunny and shaded pats, but in considerably smaller numbers compared to Limosininae sp. 1 (Tables 2.4 – 2.7). They were absent during winter and also from sunny dung pats in spring (Figs. 2.4C & 2.5C & 2.5D), although 50% of all Sphaeroceridae collected from shaded pats during spring was Sphaerocerinae sp. (Fig. 2.4D).

During summer and spring, they were recorded mainly from the shaded pats, where they were also among the earliest visitors to the dung pats. During the cooler autumn seasons,

a total of 61 individuals was collected from sunny pats at 9 hours (Table 2.7), while their numbers were extremely low on the shaded dung pats (Table 2.6). Sphaerocerinae sp. reached peak numbers at 44 hours on shaded dung in summer (Table 2.4) and after 28 hours in spring on shaded dung pats (Table 2.10).

With the exception of spring, these five Sphaeroceridae species represented a very large percentage of the total number of flies collected from the dung pats, as was highlighted in Table 2.3. Similar to this current study, many other investigations on the Diptera fauna of cattle dung, in which specific emphasis was placed on Sphaeroceridae, were done in the past (Mohr, 1943; Hafez, 1949; Papp, 1979; Rohacèk, 1983). Because these five sphaerocerids could not be identified to species level, comparisons with literature findings were impossible. Literature on Sphaeroceridae is quite extensive, but notably most studies were done in the Northern Hemisphere, and no references of any equivalent succession studies on African Sphaeroceridae could be found. In the USA Mohr (1943) found that *Leptocera* sp., for instance, usually arrived at dung pats after 15-20 minutes and gradually built up to a maximum population by the third day, after which the population decreased gradually until the end of the eighth day. This indicates that conditions in Mohr's study were probably cooler and it was possible for flies to colonize and use dung pats for a much longer period compared to the current survey. *Coproica ferruginata* and *Elachisoma nigerrima* (Haliday) for example, were found on 20-day-old dung (Hafez, 1949).

As can be seen from Tables 2.4 - 2.11, the mentioned Sphaeroceridae species occurred throughout the year. Limosininae sp. 1, for example, was especially abundant on shaded pats in summer and spring, as well as on sunny pats in autumn. Large numbers of Sphaerocerinae sp. were also collected from shaded pats in summer and spring. This is in accordance with the findings of Mohr (1943), who discovered several sphaerocerid species on cow dung during succession studies in the USA that included species such as *Leptocera* sp.; *Coprophila equinus* Fallèn, *Coprophila* sp. and *Borborus geniculatus*

Macquart. These adults were observed at all times of the year and were also among the earliest flies to visit dung in the spring (Mohr, 1943). Adult Sphaeroceridae could be observed all year round in manure-pits in Denmark, even during winter (Thomsen & Hammer, 1936). Hafez (1949) also stated that Sphaeroceridae flies in Egypt were commonly seen on dung during nearly all months of the year. Of these species *Leptocera digitata* (Duda) and *C. ferruginata* were the most abundant. Laurence (1954) mentioned the occurrence of four species of *Limosina* and four species of *Copromyza* larvae throughout the year in cow dung in Britain. Rohacèk (1983) did a very extensive succession study on Sphaeroceridae that inhabited bear excrement in the Czech Republic, and stated that adult Sphaeroceridae may occur in excrement quite irregularly to permanently, generally in small numbers. Apparently sphaerocerid species such as *C. lugubris*, *C. vagans*, *C. scutellaris*, *Copromyza atra* (Meigen) and *Halidayina spinipennis* (Haliday), are all primary inhabitants of cow dung (Rohacèk, 1983).

To illustrate the relationship observed between the number of various species attracted to droppings exposed in sun *vs* shade locations with respect to diurnal temperature maxima, the seasonal occurrence of one sphaerocerid species, Limosininae sp. 1 was considered. During summer and spring, it was more abundant on shaded pats [*e.g.* a maximum of 1281 collected from shaded pats (Table 2.4) and 306 from sunny pats in summer (Table 2.5)], while in autumn, the differences between shaded and sunny pats were just as striking – [a maximum of 202 reared from shaded pats (Table 2.6) compare to 1012 on sunny pats (Table 2.7)]. Poorbaugh (1966) also showed that the degree of habitat limitation of Diptera species during summer was related to diurnal temperatures. He found that on cool, overcast days, those species generally restricted to shady areas were found on fresh pats far from the nearest shade, and on hot, sunny days, the species generally found on sun-exposed pats were observed on shade pats (Poorbaugh, 1966). Mohr (1943) also found that the faunal composition of droppings in densely shaded woods varied from those in sunny open pastures. It became clear that Sphaeroceridae breeding activities were higher during summer than during the other three seasons. In

contrast to this, Hafez (1949) found that during spring and autumn, breeding activities of other sphaerocerids such as *L. digitata* and *C. ferruginata* attained its maximum and they usually occurred in huge swarms, especially on large manure heaps and in stables.

Sphaeroceridae were very abundant on the 3-hour-old dung in summer, indicating that they were amongst the first flies to visit and oviposit on the fresh cow pats that were put out. Hafez (1949) also found that the two sphaerocerids *L. digitata* and *C. ferruginata* were generally the first insects to appear on fresh horse dung, normally one or two minutes after defecation, while in large manure heaps, these flies could occur in large numbers on older dung. This could probably be attributed to the fact that no crust formation took place on the older dung in manure heaps.

The family **Sepsidae** consists of 21 genera and around 250 described species, found in all zoogeographical regions, with greatest diversity in the Afrotropical Region (Zuska, 1977). Zuska (1977) proposed four subfamilies, Orygmatinae, Saltellinae, Sepsinae and Toxopodinae. Sepsidae adults are small flies that spend much time on dung pats where males exhibit a characteristic fluttering of the wings (Poorbaugh *et al.*, 1968). Females normally began ovipositing into the surface of the dung when it reached the uniformly moist brown condition, usually after exposure to sun for 15 minutes, and continued to do so until the surface became blackish brown (Zuska, 1977). During this period the dung surface was soft enough for sepsids to run rapidly over it whilst thrusting their eggs into the medium (Mohr, 1943). He furthermore noted that Sepsidae females continued to deposit eggs into moist crevices and beetle holes even after it became heavily crusted (Mohr, 1943). No sepsid species are of any economic importance, although many Sepsidae, including *S. thoracica*, apparently play an important role as decomposers of animal excrement (Zuska, 1977). The genus *Nemopoda* has also been reared from a wide range of rotting media, including human excrement and vertebrate carrion (Smith, 1975). In the current study, five Sepsidae species were reared (Table 2.1), which will be individually discussed in some detail.

***Sepsis thoracica* (Robineau-Desvoidy)**

Sepsis thoracica is slender and has a dark yellowish colour. They vary in size from slightly over 2 mm to slightly under 4 mm in length. They are readily distinguished by their habit of wagging their wings as they run swiftly over the dung. This species was the most abundant sepsid species collected (35% - 99% of all sepsids) - (Figs 2.6 & 2.7). *Sepsis thoracica* was also the only Sepsidae species recorded during all seasons (Figs 2.6 & 2.7). It was also among the first species to arrive at the pats during summer, autumn and spring (Tables 2.4-2.7, 2.10 & 2.11).

Sepsis thoracica reached peak numbers within 12 hours of the dung being deposited on both shaded and sunny dung pats during the summer (Tables 2.4 & 2.5) and after 9 hours in autumn (Tables 2.6 & 2.7). During spring this species reached peak numbers on shaded and sunny pats at 24 and 9 hours respectively (Tables 2.10 & 2.11). No definite peak was noticeable during the winter, and although the numbers collected were much lower compared to the other seasons, a tendency occurred in which larger numbers were found towards the end of the 80-hour survey. No *S. thoracica* specimens were collected between 21 and 24 hours on shaded dung pats in winter (Table 2.8) and between 72 and 76 hours on the sunny pats (Table 2.9). The reason for this is uncertain, since weather conditions remained the same for the duration of the winter surveys.

***Sepsis* sp. 1**

Another sepsid species that was collected was only identified as *Sepsis* sp. 1. This species is black and about 3.5 mm in length. It represented between 2% and 19% of the total number of Sepsidae (Figs. 2.6 & 2.7), with the exception of spring, where they represented 27% of the total number collected from sunny pats (Fig. 2.7D). This species was absent from sunny pats during winter (Fig. 2.7C).

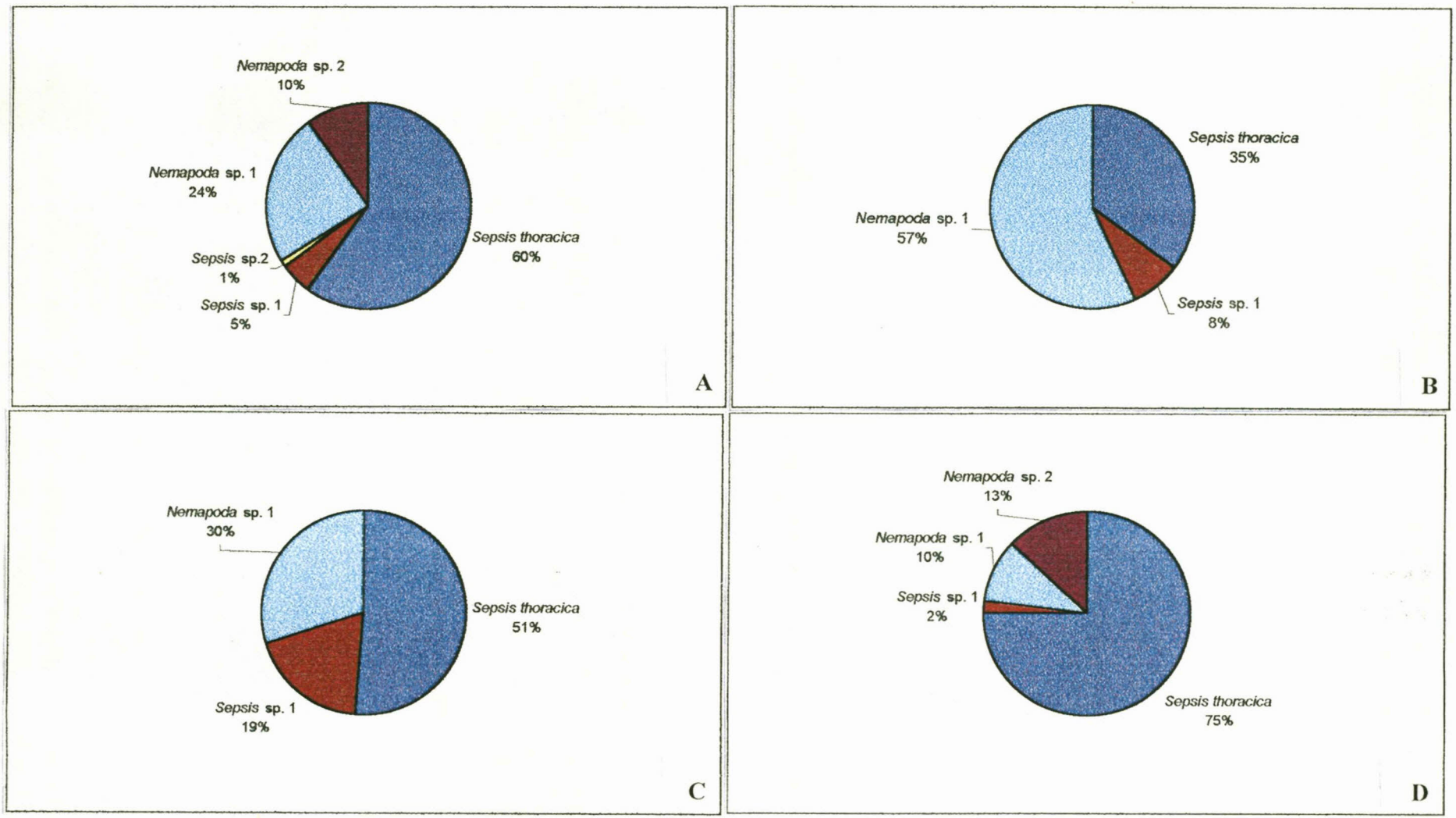


Figure 2.6: Species composition of Sepsidae collected from dung pats in the shade during four different seasons of 1992 and 1993. (Key: A – Summer; B – Autumn; C- Winter; D – Spring).

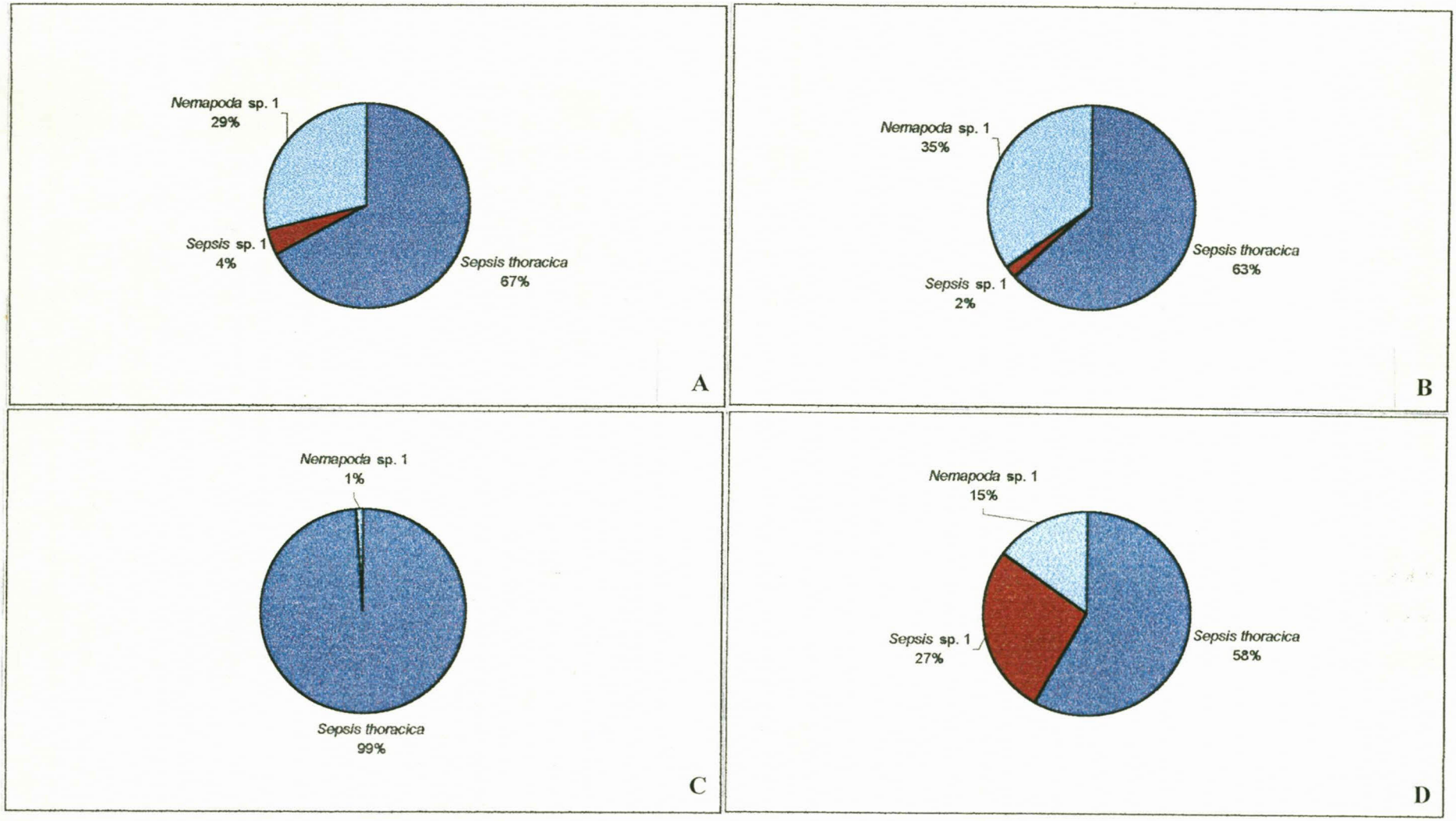


Figure 2.7: Species composition of Sepsidae collected from dung pats in the sun during four different seasons of 1992 and 1993. (Key: A – Summer; B – Autumn; C- Winter; D – Spring).

Sepsis sp. 1 showed peak numbers in summer on shaded and sunny pats after exposure periods of 9 and 12 hours respectively (Tables 2.4 & 2.5). In autumn peak numbers were recorded at 6 and 12 hours on sunny and shaded pats respectively (Tables 2.6 & 2.7), while during spring this situation occurred at 21 and 52 hours respectively (Tables 2.10 & 2.11). During all seasons a decline in numbers was noticed after 21 - 24 hours (Tables 2.4 - 2.11). Although these declines in fly numbers could also be attributed to parasitism or predation by other organisms in the dung, these inter-specific interactions were not investigated. During the autumn no individuals were collected from any of the dung pats after 24 hours (Tables 2.6 & 2.7). Environmental temperatures during the autumn were much lower towards late afternoon compared to spring temperatures, and therefore conditions during the autumn nights were probably too cold for this species to survive in the dung beyond 24 hours. This hypothesis was supported by information from the weather bureau, which recorded very low minimum temperatures during the time at which the autumn surveys were conducted.

Sepsis sp. 2

Sepsis sp. 2 is a much smaller yellowish fly compared to the other Sepsidae. It was collected from only four shaded dung pats in extremely low numbers (a maximum of only 5) during the summer seasons after the dung was exposed to fly colonization for 28 hours (Table 2.4). This species was absent during spring, autumn and winter.

Nemopoda sp. 1

Nemopoda sp. 1 is a shiny black sepsid, almost the same size as *S. thoracica* (2 - 4 mm in length). They were always very quick to appear on the dung pats - the numbers that were reared from dung exposed for only 3 hours also reflects this. *Nemopoda* sp. 1 was the second-most abundant (between 1% and 57%) of all Sepsidae collected (Figs 2.6 & 2.7). This species was collected from both shaded and sunny pats during all seasons.

Nemopoda sp. 1 reached peak numbers 12 hours after dung was deposited during summer (Tables 2.4 & 2.5). In autumn these peak numbers were reached at 12 hours on shaded pats and at 9 hours on the sunny pats (Tables 2.6 & 2.7), and during spring at 9 and 21 hours on shaded and sunny pats respectively (Tables 2.10 & 2.11). As was the case with most of the Sepsidae species collected from shaded pats during winter, their numbers were very low and at several of the sampling times, no *Nemopoda* species occurred (Tables 2.8 & 2.9). Their numbers increased towards the latter part of the winter surveys. Sub-zero temperatures were often recorded during these winter surveys which undoubtedly had an effect on the number of flies visiting and developing in the dung. Wind was hardly a factor during these periods to have influenced the number of flies on the droppings negatively.

***Nemopoda* sp. 2**

Nemopoda sp. 2 is very similar in appearance to the previous species, *Nemopoda* sp. 1, although it is a smaller species (about 3 mm in length). *Nemopoda* sp. 2 was collected only from shaded pats during summer and spring where it represented between 10% (Fig. 2.6A) and 13% (Fig. 2.6D) of Sepsidae collected. *Nemopoda* sp. 2 reached peak numbers after dung was exposed to shaded conditions for 12 hours during summer (Table 2.4), and 12 hours in spring (Table 2.10). Conditions during the other two seasons were probably not conducive for the development of this species due to unfavourable temperature or light conditions.

It was observed that Sepsidae species' choice between shaded and sunny pats varied considerably during the different seasons. During summer and spring, large numbers of Sepsidae were collected from shaded locations. However, during winter, exactly the opposite situation was observed. Poorbaugh (1966) demonstrated that these differences in environmental tolerance limits of fly species may account for their differential numerical occurrence in sun and shaded habitats. Furthermore, since the varying ratios

of abundance of sun and shade occurrence were obviously correlated with differing diurnal temperatures, the degree of habitat restriction of various species was probably directly related to their temperature and humidity tolerance limits (Landin, 1961). Mohr (1943) also found that adult females of *Sepsis violacea* Meigen bred during warmer summer periods, whereafter hibernation took place in the puparium within the dung pats during winter. Laurence (1954) also found Sepsidae in Britain to be present on cow dung only during the summer periods.

Darker Sepsidae species such as *Sepsis* sp. 1 and *Nemapoda* sp. 1 were more abundant on shaded pats, while the lighter species such as *S. thoracica* and *Nemapoda* sp. 2 were sampled mainly from the sunny pats. Conditions on sunny pats in summer were not as favourable compared to those in the shade, for instance, yet the lighter coloured species preferred these sunny pats to the shaded ones. This phenomenon could be attributed to a camouflage effect that these species displayed most probably to avoid predators, but it could also be as a result of thermo-regulation among the flies.

During the warmer seasons *e.g.* summer and spring, peak numbers were reached much sooner compared to winter, where peak numbers were only reached after 48 h to 76 h. This phenomenon was clearly illustrated in Table 2.2. The reason for this was most probably the lower winter temperatures that had a retardation effect on the development of immature stages of all flies. Furthermore, among some of the Sepsidae collected (*e.g.* *Sepsis* sp. 1 and *Nemapoda* sp. 1), a general trend was found where peaks of abundance were reached much sooner on sunny pats compared to the shaded ones. This was indicative of the fact that pats in the sun probably became drier much quicker and were therefore ready for colonization and oviposition by the sepsids long before the shaded dung pats were. Because conditions in the sun were warmer, fly larvae probably also developed faster, which enabled them to complete their life cycles before the sunny pats became too dry. This would have ensured successful survival, while the moisture content

of the shaded pats remained higher for longer periods, allowing development of flies even when eggs were oviposited on the dung much later than on the sunny pats.

Muscidae is a large family, represented in all regions of the world, consisting of nine subfamilies (Ferrar, 1979). A number of synanthropic species have extended their distributions with man, and the house fly, *Musca domestica* Linnaeus for instance, is cosmopolitan (Ferrar, 1979). Most Muscidae have larvae that may be facultatively saprophagous or facultatively predacious on other organisms (frequently other fly larvae) within the medium in which they are living (Ferrar, 1979). These saprophagous Diptera species generally have three larval instars, as is normal in Cyclorrhapha (Ferrar, 1979). A total of ten different Muscidae species were reared during this study (Table 2.1), most of them in small numbers, especially during the autumn and winter months (*O. perronii* excluded) (Tables 2.6 - 2.9).

***Musca* (*Eumusca*) *xanthomelas* Wiedemann**

Musca xanthomelas (African face fly) occurred during all four seasons and represented between 1% and 46% of all the Muscidae collected (Figs. 2.8 & 2.9). During summer and winter, this species represented 46% and 37% of all Muscidae reared from sunny pats respectively (Figs. 2.9A & 2.9C), while on shaded pats in winter, they also represented 75% of the Muscidae collected (Fig. 2.8C). This high percentage might be misleading, since the number of flies collected on shaded pats during the winter was very low (see Table 2.8). Most of the *M. xanthomelas* were collected in summer where peak numbers were found at 68 hours on the shaded pats (Table 2.4) and at 3 hours on the droppings which were placed in the sun (Table 2.5). During the other three seasons, very few individuals were collected from both shaded and sunny pats (Tables 2.6 - 2.11).

Musca xanthomelas, it seems, could be of some economic importance, since Nevill & Sutherland (1987) identified this species, together with some other muscids such as

Musca lusoria Wiedemann and *Musca nevilli* Kleynhans, to be a vector of a filarial worm *Parafilaria bovicola* Tubangui in South Africa. Barnard *et al.* (1990) initially implicated *M. xanthomelas* in the epidemiology of wildebeest-derived malignant catarrhal fever in South Africa, but later discovered that these flies were not responsible for the mechanical transmission of this disease. Because they were collected in such small numbers during this study, they were not considered a threat to the cattle population at the experimental pasture.

***Musca* (*Philaematomyia*) *crassirostris* Stein**

Musca crassirostris is smaller than *M. xanthomelas* and was collected from several shaded pats only during the summer and autumn (Figs 2.8A & 2.8B). Only about 1% of Muscidae collected were *M. crassirostris*. They were absent during the winter (Tables 2.8 & 2.9) and spring (Tables 2.10 & 2.11). According to Ferrar (1979), *M. crassirostris* and other species such as *Musca conducens* Walker and *Musca inferior* Stein have teeth on their probosci, and rasp soft tissue of their hosts to promote blood flow. Males of these species feed on nectar of flowers, sweet exudations of paspalum grasses infected with ergot, and on honeydew secreted by aphids and coccids (Cuthbertson, 1933). In Zimbabwe fresh cattle dung, and occasionally human faeces were recorded by Cuthbertson (1932) as preferred breeding material for *M. crassirostris* and *M. xanthomelas*.

***Phaonia* sp. 1 & sp. 2**

The subfamily Phaoniinae also consists of two tribes, namely Brontaeini and Phaoniini (Ferrar, 1979). Two *Phaonia* species were collected from shaded dung pats during the summer where they only represented about 1% of the Muscidae collected. Both species were absent from all dung pats during autumn (Figs 2.8B & 2.9B). During winter, *Phaonia* sp. 1 represented 25% of Muscidae collected from shaded dung pats only,

although their numbers were very low (Fig. 2.8C & Table 2.8). In spring, *Phaonia* sp. 1 was also reared from sunny pats (only 1% of all Muscidae collected) (Fig. 2.9D), but was absent from the shaded pats (Fig. 2.8D). *Phaonia* is a very large genus, with a wide variety of breeding places (Ferrar, 1979) and probably most or all species are obligate predators of other insects (Skidmore, 1973).

Muscinae sp. 1 & sp. 2

Two other Muscidae species, with very distinct black spots on their abdominal regions, were encountered which were only identified as Muscinae. The subfamily Muscinae has two distinct tribes, Muscini and Mesembrinini (Ferrar, 1979). The two Muscinae species occurred during all four seasons, except on shaded pats in winter, and represented between 1% and 78% of Muscidae collected from both sunny and shaded pats (Figs 2.8 & 2.9). Their numbers were generally very low and their occurrence on the droppings was extremely irregular. Larvae of most genera in the Muscini tribe are saprophagous in dung, except those of *Pyrellina*, which apparently breeds in rotting fruit (Pont, 1973).

***Orthelia perronii* (Robineau-Desvoidy)**

Orthelia perronii is a greenish metallic muscid that was initially confused with greenbottles or blow flies. According to Zumpt (1953), these "false greenbottles" *Orthelia*, which also has a sharply bent fourth vein like *Lucilia*, differs from that genus in that the frons and jowls are also metallic green and this species is usually also associated with excrement. *Orthelia perronii* emerged in large numbers from shaded pats in summer (Fig. 2.8A & Table 2.4) and autumn (Fig. 2.8B & Table 2.6) and from both shaded and sunny pats in spring (Figs. 2.8D & 2.9D, Tables 2.10 & 2.11). They represented between 91% and 97% of all Muscidae collected (Figs. 2.8 & 2.9). This species was absent during the winter.

This was also the only Muscidae species where a succession pattern could be followed. Peak numbers were reached after shaded dung was exposed for 9 hours in summer and 32 hours during autumn (Tables 2.4 & 2.6), although none was collected from any of the sunny pats during summer or autumn (Tables 2.5 & 2.7). However, during spring they occurred on both shaded and sunny pats, where peak numbers were reached at 24 hours and 32 hours respectively (Tables 2.10 & 2.11). This clearly indicates that temperature and possibly also moisture content of dung played important roles in determining feeding and oviposition habits of the females.

***Orthelia nudissima* (Loew)**

Orthelia nudissima is another muscid species that was only collected from two shaded dung pats (Fig. 2.8) and a few sunny dung pats during summer (Fig. 2.9 & Tables 2.4 & 2.5), but was absent during all other seasons. It only represented between 1% and 2% of all Muscidae species that were sampled from the dung pats.

***Musca* sp. 1 & sp. 2**

Interestingly, two other Muscidae species, indicated as *Musca* sp. 1 and *Musca* sp. 2, were only collected from both shaded and sunny pats during autumn and from sunny pats in spring (Figs 2.8 & 2.9). They appeared to be absent from pats during summer and winter months, as well as shaded pats in spring (Tables 2.4 - 2.11). Between 1% and 5% of the muscid species collected were either *Musca* sp. 1 or sp. 2.

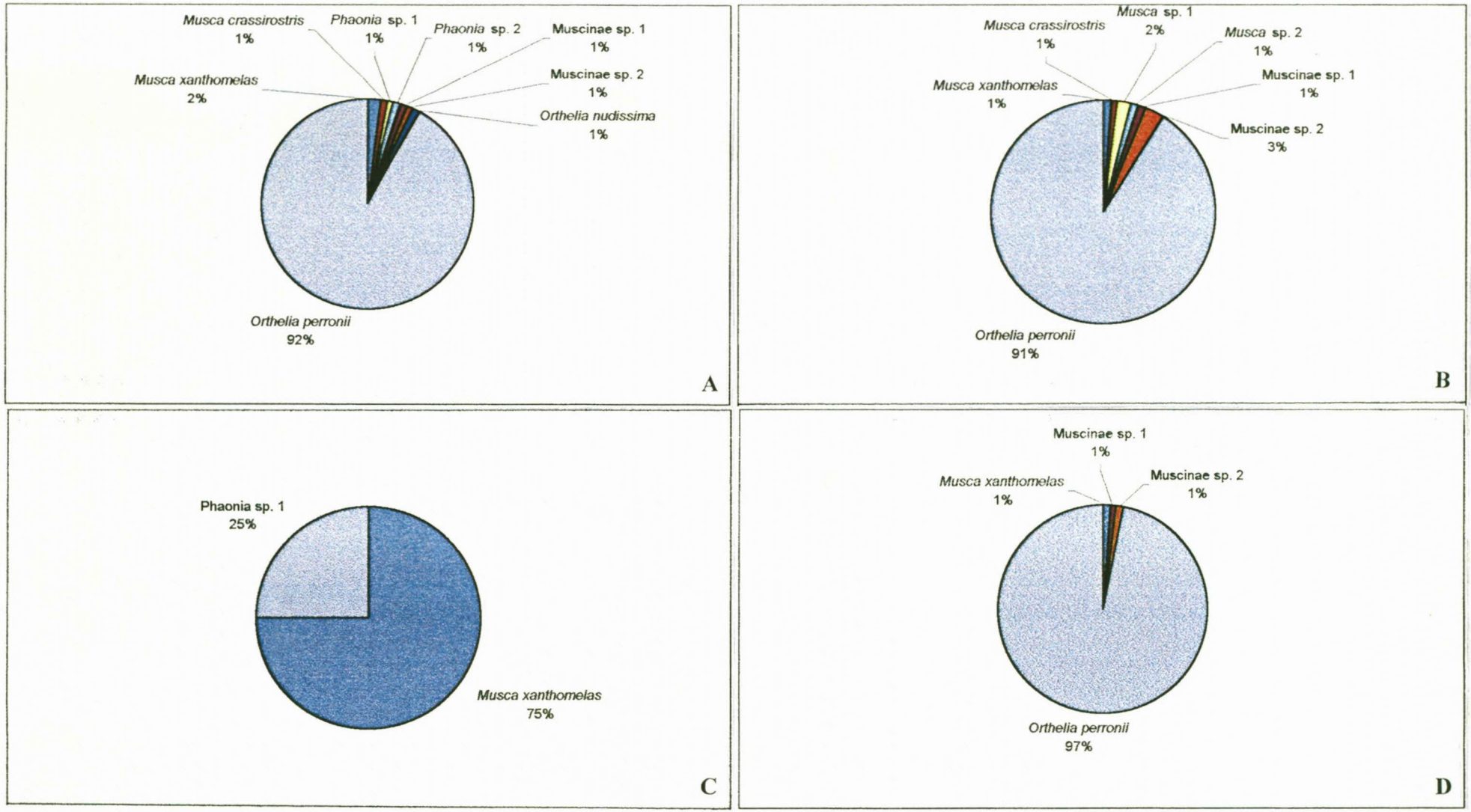


Figure 2.8: Species composition of Muscidae collected from dung pats in the shade during four different seasons of 1992 and 1993. (Key: A – Summer; B – Autumn; C- Winter; D – Spring).

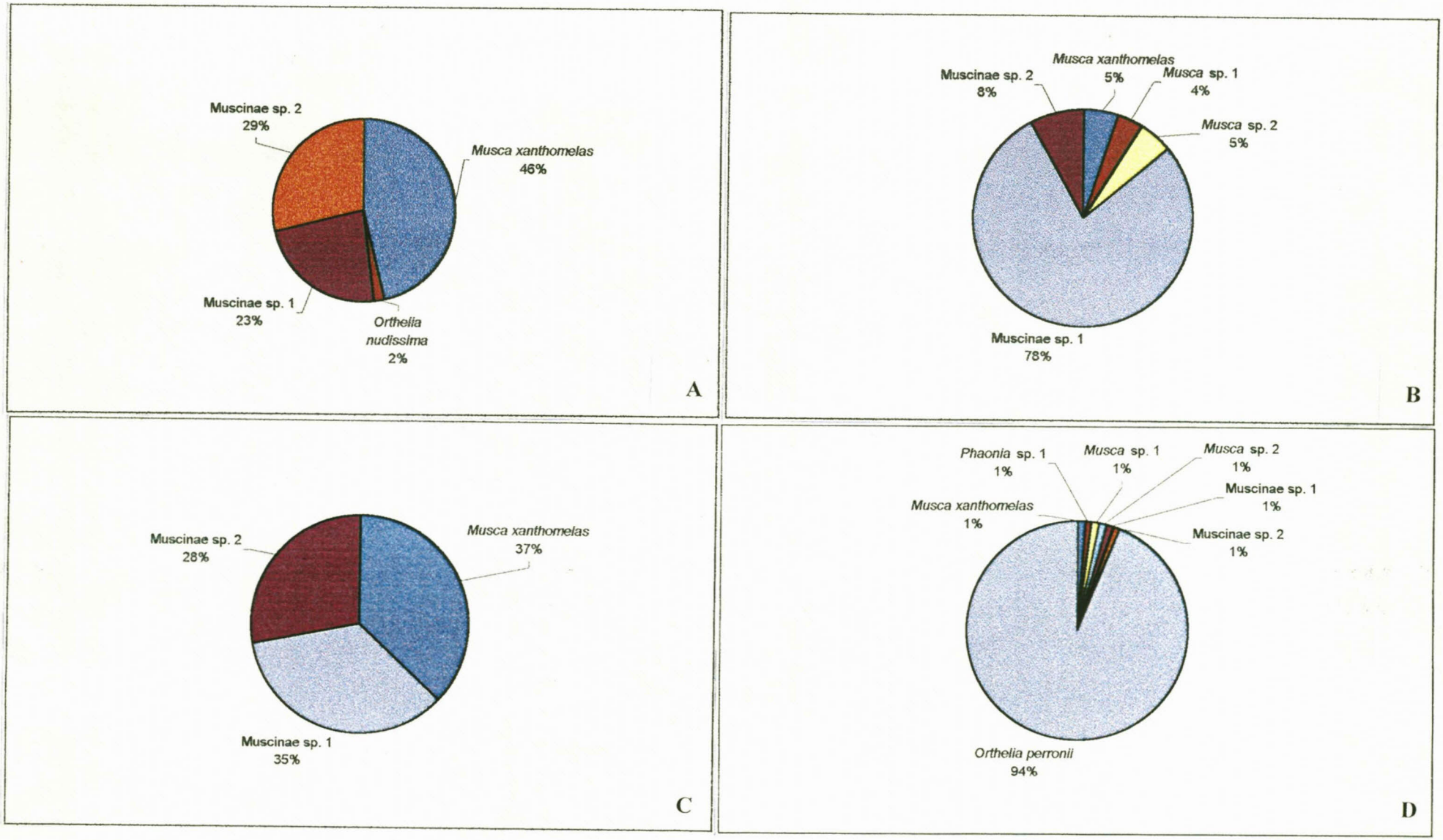


Figure 2.9: Species composition of Muscidae collected from dung pats in the sun during four different seasons of 1992 and 1993. (Key: A – Summer; B – Autumn; C- Winter; D – Spring).

In comparison with the Sphaeroceridae and Sepsidae, the percentage of Muscidae collected, in particular *M. xanthomelas* and *M. crassirostris*, was generally much lower, especially during autumn and winter (Table 2.3). This could be attributed to the larger size of the Muscidae larvae, which were not able to develop in such large numbers from the same sized dung pats as the smaller fly larvae. Results of the census sampling (Tables 2.4 - 2.11) showed that several of the muscoid Diptera such as *M. xanthomelas*, *M. crassirostris* and *O. perronii* were attracted to dung during the first three hours of exposure. Populations of these flies were therefore consistently sampled, especially on shaded dung pats in summer and sunny pats in spring. Literature on the biology and taxonomy of Muscidae is very extensive, and is therefore impossible to cover entirely in this chapter. However, most studies involving Muscidae centered around pest species such as *H. irritans*, *M. autumnalis*, *Musca vetustissima* Walker, *Stomoxys calcitrans* (Linnaeus) and *Musca tempestiva* Fallèn, that were all early visitors to droppings in the field (Hammer, 1941; Mohr, 1943; Poorbaugh, 1966). The current results were in accordance with those of Poorbaugh *et al.* (1968) who found that Muscidae flies such as *Morellia micans* (Maquart) and *Orthelia caesarion* Meigen were both primary inhabitants of cattle dung because they were reared from droppings that were exposed for only three hours. Similarly Merrit & Anderson (1977) reared eight different Muscidae species from dung pats collected at different pasture and rangeland ecosystems in California, USA. During this present study, no *M. domestica* was collected during any of the seasonal surveys. Papp (1971) stated that *M. domestica* only visits dung pats, but does not oviposit there. In the USA, Mohr (1943) found *M. domestica* to be highly irregular visitors to droppings, being slightly more common during dry or cool seasons, evidently taking moisture and food. No *M. domestica* larvae were sampled from the dung either (Mohr, 1943). Amano (1985) also found that *M. domestica* does not breed in isolated cow pats and breed mainly in garbage and a variety of other rotting media associated with human habitation, although it does use large manure heaps as breeding sites.

Sarcophagidae is a large family, of worldwide distribution, that is divided into three subfamilies - Macronychiinae, Paramacronychiinae and a smaller subfamily Sarcophaginae (Ferrar *et al.*, 1975). At times it has been treated as a subfamily of Calliphoridae, but is now regarded as a distinct family (Ferrar *et al.*, 1975). Sarcophagidae adults are large grey-black flies with brick-red eyes, commonly referred to as flesh flies, since a number of species breed in carrion (Ferrar *et al.*, 1975). Some species can be harmful, such as the genus *Wohlfahrtia*, that contains several species whose larvae are apparently obligate feeders in mammalian tissue, subcutaneously or in wounds, whilst other species in the genus have saprophagous larvae (Ferrar *et al.*, 1975). Some species may be beneficial, as a number of Sarcophagidae parasitize locusts and are of significance as biological control agents (Ferrar *et al.*, 1975).

Only one Sarcophagidae species, *S. cruentata*, was collected from both shaded and sunny pats during summer (Tables 2.4 & 2.5), and from sunny pats in winter and spring (Tables 2.9 & 2.11), but overall only low numbers were recorded. They were absent during autumn (Tables 2.6 & 2.7). These observations are in accordance with those of Poorbaugh *et al.* (1968) who stated that Sarcophagidae are predominantly found in sunny locations. Mohr (1943) also showed that adult sarcophagids appeared during warm weather and continued breeding until the frost set in. As a result of this, very few individuals were collected from sunny pats during winter probably because conditions were too cold for them during these periods. This is in accordance with findings by Zaharova (1971) who were able to show that during cold and rainy periods, larvae of *Sarcophaga scoparia* Pand pupated and entered diapause. On the other hand, Hanski & Kuusela (1980) also stated that the onset of pupal diapause in Sarcophagidae is under complex thermal and photoperiodic control. Denlinger (1978) showed that in tropical areas of the USA, *Sarcophaga* sp. usually develop continuously throughout the year, but exceptionally cold weather may induce pupal diapause in at least some individuals.

The occurrence of *S. cruentata* was also very irregular and therefore it was difficult to establish any clear succession pattern. However, during summer some *S. cruentata* were reared from dung that was exposed for only three hours, indicating that they were also among the early visitors to the droppings in the shade (Table 2.4). Poorbaugh *et al.* (1968) also found that Sarcophagidae females generally visited pats to deposit larvae during the first two to three hours after dung was exposed. Mohr (1943) observed *Sarcophaga* species larvapositing in dung cakes exposed from only five minutes up to three hours, but that a peak of abundance was at about half an hour. Larvae develop rapidly and pupate before any predaceous maggots can kill many of them (Poorbaugh *et al.*, 1968).

Towards the end of autumn, pastures began to dry and the typical dry-season conditions of the South African highveld began to prevail. During this period, average day and night temperatures started to drop as well. Although there appeared to be little change in faunal composition, some species disappeared until the onset of spring (*e.g.* Limosininae sp. 4; Sphaerocerinae sp.; *Sepsis* sp. 1; *Nemapoda* sp. 2; *M. crassirostris*; *Phaonia* sp. 1; *O. perronii* and *O. nudissima*). Fly activity during winter also decreased considerably, as could be seen in the winter surveys (Tables 2.8 & 2.9). It therefore seems as if there were two rather distinct groups, a summer and a winter complex, and a few species characteristic of spring and autumn only (*e.g. Musca* sp. 1 and *Musca* sp. 2). This is in contrast with the findings of Poorbaugh (1966) whose studies showed that two other groups existed, namely dry-season and wet-season faunal complexes. Perhaps this distinction can be attributed to the North Californian coastal climate where his studies were conducted and which differ vastly from that of the central Free State. Mohr (1943) found three groups in Illinois, USA, *i.e.* a summer and winter complex and those species occurring only during spring and autumn. Hammer (1941) also found three groups in Denmark. Laurence (1954) stated that in England there was not one coprophagous community but a series of coprophagous communities that replaced one another during the year.

At the experimental pastures, all the major Diptera were attracted in the first 30 minutes after the pats were exposed. This was possible because all pats were placed out at 8:00 in the morning, a time when fly activity was high (Rohacèk, 1983), especially during summer. Pats collected later in the first day seemed to lose their attractiveness as the day progressed, but there was no distinct surface succession of species as was reported by Mohr (1943) in the USA or Hammer (1941) in Denmark. Most of the Sphaeroceridae, Sepsidae and *O. perronii* (Muscidae) might have preferred very fresh dung pats, because they were all reared from droppings which were exposed to fly attraction for only three hours.

It appeared as if strong flying flies such as Sepsidae and Muscidae, for example, were quick to appear on sunny pats early in the day, no matter where they were dropped. The slow-moving flies such as smaller Sphaeroceridae species generally occurred in large numbers on pats that were placed near vegetation. This is in agreement with observations made by Poorbaugh (1966), who showed that there is much variation in the dispersal potential of the different species inhabiting cow pats and in their relative abilities to reach fresh pats located away from resting sites. Some species with limited powers of dispersal probably remained at rest and were activated only by the smell of fresh dung if it was dropped nearby, whereas others were actively flying in search of fresh pats when they were gravid (Poorbaugh, 1966).

While these succession studies were conducted, it was observed that many fly species accumulated on nearby grass and occasionally some individuals touched the surface of the dung lightly. Only after a couple of minutes when dung became dry enough, did flies move unto the pats. Sepsidae and Muscidae were always the first to arrive at dung pats in large numbers, but smaller Sphaeroceridae which were not always easy to see, were also very abundant. Papp (1971) also found that these three fly families, Sphaeroceridae, Sepsidae and Muscidae played an important role as larvae in utilizing cattle droppings as larval rearing medium.

From the results presented in Tables 2.4 - 2.11, a noticeable drop in the number of flies that emerged from pats was observed towards the end of each experimental period. This trend was also observed by Mohr (1943) who found that flies usually attain continuous representation and showed a distinct and gradual increase to a peak of abundance followed by a decline. Theoretically, the number of flies that emerged from each dung pat should stabilize after the first day because of the crust formation that prevented the flies from laying eggs, and very few flies were then also seen on droppings after the first day. The drop in the number of flies that emerged from dung pats that were left in the field for more than two days could be attributed to predation by other organisms such as ants, birds and meerkats that sometimes destroyed the dung pats completely. This happened during all eight surveys conducted, and during the summer some of these pats even suffered extensive damage after 52 hours. Birds and animals were seen damaging the dung pats to such a degree that very little remained to be taken back to the laboratory. Sometimes ants were seen attacking the fly maggots and carrying them away. Other predators such as Hymenoptera might also have contributed to this phenomenon. In similar studies in the USA, Mohr (1943) found that this is no reason for concern, since the predominant insects of the first microseral stage, especially the higher muscoid flies, arrived at fresh dung soon after it was dropped and the major colonization of fresh pats was completed within the next 24 hours. The first few pats collected would therefore give a clear indication of the flies that utilized undisturbed dung pats. This was another reason for not conducting the succession studies beyond an 80-hour period.

During this study, all artificial dung pats of the different seasons were put out at the same time. This might have influenced the numbers and variation in faunal composition of any individual dung pat. The reason for this is that from a quantitative aspect, the abundance of gravid females of a given species, which might have reached any one pat, depended not only on the general abundance of species in the potential attractive area, but also on how many pats were dropped at a specific time (Poorbaugh, 1966). He also found that if several cattle should stand up simultaneously in an area and result in several

pats being dropped at the same time, the number of eggs deposited in each pat by any fly species would undoubtedly diminish (Poorbaugh, 1966). However, this does not pose a serious constraint to any of the results obtained, since experimental procedures remained the same throughout the trial and the same number of pats were placed out at the experimental pastures each time.

These succession studies furthermore indicated that all fly species that develop in these dung pats have rapid development rates. However, a few cases have been reported where species such as the stratiomyiids *Sargus* sp. and *Microchrysa* sp., and the midge, *Camptocladius* sp., have a much longer period of development, *i.e.* 60-100 days or more, and in the case of Stratiomyidae, the pat may disintegrate before development is completed (Laurence, 1955). Hammer (1941) recorded larvae of *Sargus* sp. surviving into the second year after deposition of the pat. No such cases were encountered during the current survey.

The results of these field and laboratory studies of quantitative sampling and experiments at Hebron presented herein provide a fair description of the dynamics of the fly community which occurred as larvae in undisturbed cattle droppings in the central Free State. The predominant fly species were active on artificially exposed fresh dung that remained attractive for several hours. It also became evident that not as many fly species utilize cattle dung in the Free State as was initially thought. A total of 21 different fly species were reared from the collected dung pats that were put out in the field. Some families such as Sepsidae and Sphaeroceridae were more abundant compared to others such as Muscidae and Sarcophagidae. Due to the nature of this study, Sphaeroceridae was of particular interest. Unfortunately only five presumably new species were collected. No *C. vagans* or *C. hirtula* species were collected from the succession studies conducted at Hebron. Seasonal variation definitely played an important role in establishing the numbers and variety of fly species that utilized cattle dung pats.

There was a distinct difference between the habitat of undisturbed cattle droppings as they lie in the field and that of cattle dung disturbed either by man and heaped into manure piles or trampled by cattle and mixed with urine. Studies at the feedlot showed a very small fly species diversity in comparison to those on undisturbed cattle droppings (see Chapter 7).

Future investigations into the fauna of undisturbed cattle droppings in the Free State could be extended to include comparative analysis of the individual and collective population fluctuations with weather and habitat data. This could eventually provide considerable insight into the natural histories of these coprophilic insects. Possible population interactions between coprophagous fly larvae and predaceous species that could have accounted for some of the observed population fluctuations of abundance could be considered as well.

CHAPTER 3

COMPARATIVE STUDY ON THE EFFECT OF TEMPERATURE ON THE LIFE CYCLES OF *COPROICA VAGANS* AND *COPROICA HIRTULA*

3.1 INTRODUCTION

A number of temperature studies by various authors have been carried out on a variety of dipteran species, *e.g.* Larsen & Thomsen (1940); Hammer (1941); Feldman-Muhsam (1944); Wang (1964); Lee & Denlinger (1985a) and Amoudi (1993). The eggs of the house fly, *M. domestica*, hatched at 10°C, but larval growth was inhibited at this temperature (Larsen & Thomsen, 1940) and below 4°C the larvae died (Feldman-Muhsam, 1944). On the other hand, Melvin (1934) showed that house fly eggs were able to hatch at temperatures higher than 40°C. Lee & Denlinger (1985a) determined low temperature tolerance of *Sarcophaga crassipalpis* (Walker) and found that diapause-destined larvae could tolerate exposure to temperatures of -10°C for short periods. Fredeen & Glen (1970) studied the influence of temperature on the Sphaeroceridae species *L. caenosa,* and were able to show that the optimum development temperature was 17°C, while the life cycle duration at this temperature was 30 days.

The apparent lack of information on the biology and especially the temperature tolerance of both *C. vagans* and *C. hirtula* prompted a comparative temperature study. This study was undertaken with the following key questions in mind:

(1): What is the percentage survival and duration of each development stage in the life cycle of the two Sphaeroceridae species at constant and fluctuating temperatures?

(2): What is the optimum survival temperature for these two sphaerocerid species required to maintain healthy laboratory colonies?

(3): What is the temperature threshold of development for these two species?

3.2 MATERIAL AND METHODS

3.2.1 Establishment of laboratory colonies

The main research areas were at Blokhuis feedlot near Harrismith (28° 19'S; 29° 07' E) and Sparta feedlot near Marquard (28° 35' S; 27° 29' E) in the Free State. Adult Sphaeroceridae collected at these two feedlots was used to establish laboratory colonies. At these feedlots, the two species *viz. C. vagans* and *C. hirtula* were present with *C. vagans* the dominant species. Blokhuis feedlot covered an area of approximately 30 hectares where between 10000 and 18000 cattle were kept (Fig. 3.1 & 3.2). Although the feedlot was surrounded by cultivated land and natural pasture, no vegetation was present inside the feedlot camps. Adjacent to the cattle camps was an area where 5000 sheep were kept. There were also three earth dams permanently filled with run-off water from the feedlot and dung which was dumped there when the camps were cleaned annually, mainly during the winter months. Sparta feedlot was much larger and approximately 30000 to 45000 cattle were kept at this site. General conditions at these two feedlots were very similar.

The flies were sampled with sweep nets, transferred to gauze insect-rearing cages (35 x 35 x 35 cm) and transported to the Department of Zoology and Entomology at the University of the Orange Free State, where the species were separated. The flies were anesthetized with CO_2 and separated by hand under a Zeiss stereomicroscope to ensure separate and pure colonies of *C. vagans and C. hirtula*. Fresh dung from the feedlot was supplied to the adult flies as breeding medium and was placed in plastic containers (33 x 22 x 6 cm.). Flies were then allowed to oviposit on the dung and after three days, the containers were removed and covered with fine nylon stockings (Fig. 3.3). This was done to ensure that no other coprophagous flies oviposited in the same dung and also to

prevent the next generation of adult flies from escaping. To prevent the dung from drying out, it was kept moist by spraying distilled water onto the dung on a daily basis.

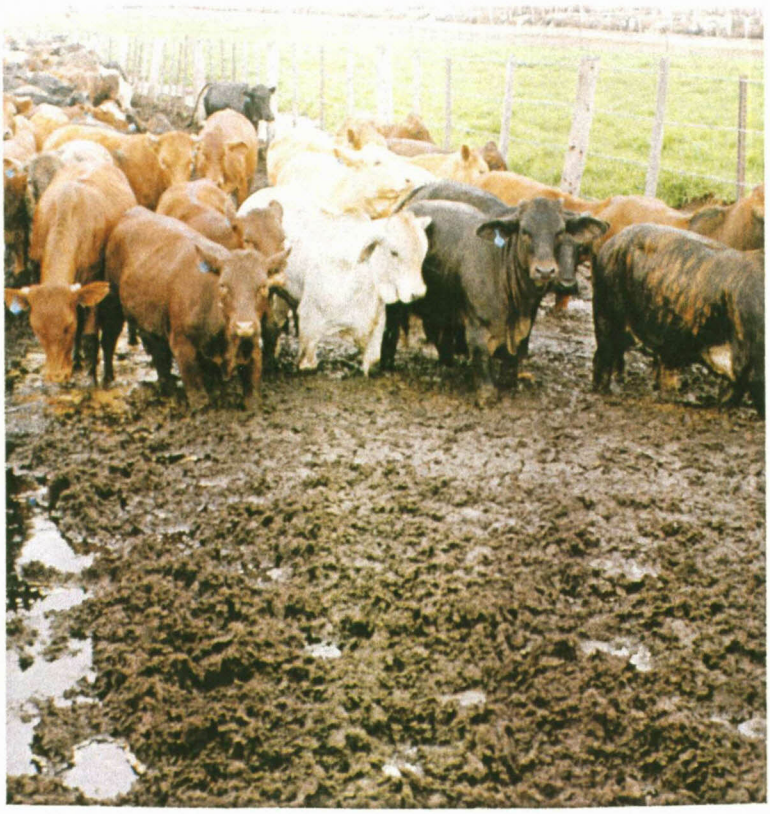


Figure 3.1: Blokhuis feedlot during wet summer conditions.

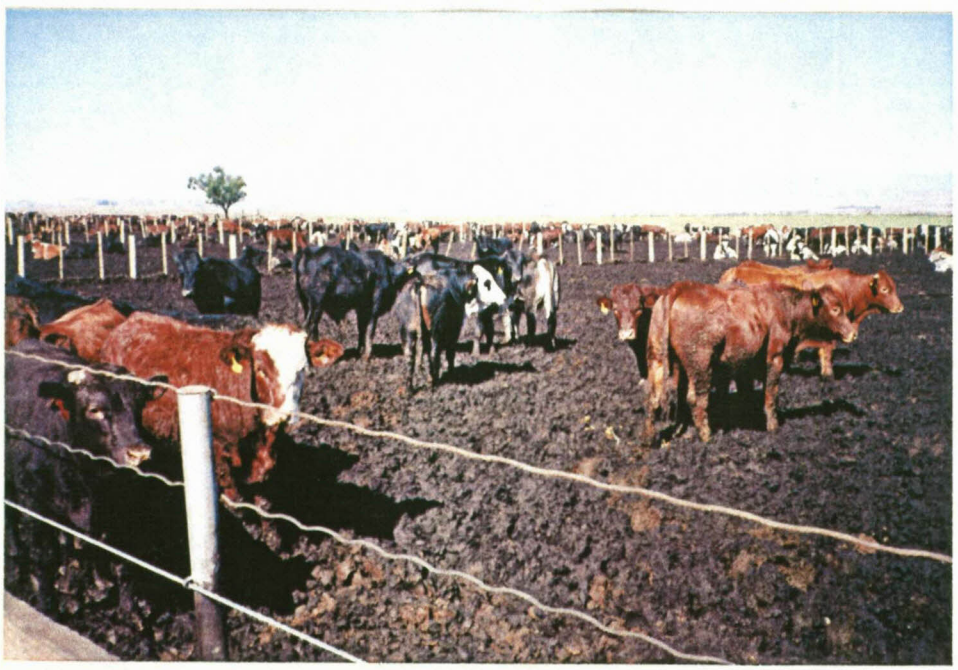


Figure 3.2: Blokhuis feedlot near Harrismith, eastern Free State.

Figure 3.3: Plastic containers covered with nylon stockings in which the laboratory colonies were maintained.

The plastic containers with the flies were kept in a temperature and humidity controlled room at a constant temperature of 27 ± 1°C and a relative humidity of 80 ± 5%. A day-night cycle of 12 hours light (at a light intensity of 700 watt) and 12 hours dark, which included an hour dawn at 06:00 and an hour dusk at 18:00, was maintained.

Cotton wool was initially moistened with a 10 % sugar solution or 10 % molasses and placed inside the cages as food for the adults, but this proved to be unnecessary. Adult flies obtained nourishment from the dung itself. Fresh dung from the feedlot was not always available and therefore older dung had to be used. To avoid possible contamination with other Diptera or coprophagous insects, the dung was frozen or autoclaved, then ground to a fine powder and wetted with distilled water. This "sterilized dung" proved to be equally efficient as a rearing medium. However, dung containing a high percentage of fibre proved to be less efficient (see Chapter 6). During a later stage

of the study it was decided to collect dung at the feedlot, bring it back to the laboratory and freeze it at -25°C. When needed, the dung was thawed for 24 hours and then presented to the flies. This method was also very successful. Each successive generation of flies was transferred to newly prepared plastic containers with fresh dung.

3.2.2 Experimental procedure

The experimental procedures described here applied to all development stages, egg, larvae, pupae and adult flies. All the temperature experiments were done in electronically controlled incubators set at constant temperatures ranging from 0°C to 48°C at 6°C intervals and a day-night cycle of 12 hours light and 12 hours dark. Apex vials No. 8 (75 x 25 mm) were used as experimental containers. These vials were provisioned with wet sterilized cattle dung to a depth of two centimetres. The dung was sterilized by freezing it at -25°C for at least two weeks to ensure that the dung was free from any other living organisms which could have influenced the results.

To prevent desiccation of the dung, especially at high temperatures, a few millilitres of distilled water was sprayed onto the dung daily. However, care was also taken not to add too much water to the dung. The distilled water was kept inside the incubators at various temperatures to prevent any temperature fluctuations when added to the dung. Larsen & Thomsen (1940) emphasized that it is important to keep the moisture content of the dung high, as desiccation tended to retard the development of immature stages. An open container filled with distilled water was also kept inside each incubator to maintain a constantly high relative humidity and to slow down desiccation. The relative humidity inside the incubators was not measured during these temperature studies.

Observations were made once a day, but towards the end of the pupal stage when many adult flies emerged simultaneously, they were made every 12 hours at approximately 08:00 and 20:00. Ten vials were used in each trial for each of the two species and the

experiment was repeated three times. Glass vials were used because plastic vials proved to be poor heat conductors. The development time of the different stages at each temperature regime, as well as the percentage survival of each stage, were determined for both *C. vagans* and *C. hirtula*.

The data were subjected to probit analysis (SAS Institute 1985) where overlapping 95% confidence intervals were considered not significantly different.

3.2.3 Eggs

A single female was put in each vial to oviposit. The vials were closed with perforated stoppers to prevent the flies from escaping, but simultaneously allowing air ventilation into the vials. All the vials were kept at 24 ± 1°C for an initial two-day period to allow the females to oviposit. The females were then removed from the vials and the number of eggs was counted and allowed to hatch. Eggs that were oviposited on the glass above the dung were removed and discarded.

3.2.4 Larvae

Once the percentage hatching was determined, 50 first instar larvae were removed from each vial and transferred to another set of similarly prepared vials. However, at the extreme temperature regimes of 12°C and 36°C, very few eggs hatched and additional first instar larvae had to be taken from the laboratory colonies for this experiment. At temperatures of 0°C, 6°C, 42°C and 48°C, the survival of larvae and pupae were not tested because the eggs did not hatch at these extreme temperatures.

3.2.5 Pupae

Fifty newly formed pupae were introduced into a third set of prepared vials (see 3.2.2) and exposed to the different temperature regimes in the incubators. These pupae originated mainly from the larvae reared in the larval experiment (see 3.2.4). Unfortunately at some of the temperatures, especially the extreme ones, 12°C and 36°C, most of the larvae died and more pupae had to be taken from the laboratory colonies. These fresh pupae were carefully selected to ensure that they were not older than 12 hours. These pupae appeared much softer and lighter in colour compared to the older pupae.

3.2.6 Life expectancy

The life expectancy of the adult flies was determined by collecting newly emerged adults with an aspirator from the laboratory colonies and transferring them to the prepared vials (see 3.2.2.). Ten vials were used in each trial, and each vial contained 10 flies. However, no effort was made to determine the sex of the individuals, since the life expectancy of adult flies in general was determined.

3.2.7 Fluctuating temperatures

The influence of fluctuating environmental temperatures during the summer and winter months were also determined by exposing the different development stages to natural environmental temperature regimes. The daily temperature, including the minimum and maximum for the duration of the experiment were obtained from the Weather Bureau at the Bloemfontein Airport. The experimental procedure was the same as described in 3.2.2. The only exception was that the glass Apex vials were placed outside the laboratory (approximately 50 metres away) on the UOFS campus and exposed to natural fluctuating temperatures. These experiments, as well as those conducted at constant

temperatures, were executed simultaneously to ensure that the same Sphaeroceridae populations were used in both experiments.

The rearing medium was initially stirred very carefully once a week to ensure that the moisture content remained the same throughout the medium. Later, vermiculite was mixed with the rearing medium for the same reason. In similar experiments, Goodhue & Cantrel (1958) found that at lower temperatures the moisture content of the media increased due to the moisture excreted by fly larvae just before pupation. They also found that vermiculite absorbed the excess moisture and kept the moisture content of the dung relatively constant. Care was also taken to provide adequate ventilation inside the incubators. It was observed that without sufficient oxygen, the larvae tended to leave the dung and pupate on the glass sides of the vials where they eventually died.

3.3 RESULTS AND DISCUSSION

3.3.1 Establishment of laboratory colonies

At the beginning of the experiment, the rearing room was kept at 27 ± 1°C, which was based on the average summer temperature at Blokhuis feedlot. Subsequent temperature experiments revealed that the optimum rearing temperature was 24°C for *C. vagans* and 30°C for *C. hirtula* (see Fig. 3.18). Various light-dark regimes were tested, but 12 hours light and 12 hours dark seemed to be the preferred light cycle for oviposition (see Chapter 5).

The colonization of Sphaeroceridae in the laboratory is important for the successful elucidation of certain aspects of the biology of *C. vagans* and *C. hirtula*. Many interpretations of ecological phenomena observed in the field are based on observations made under controlled laboratory conditions. Wilson & Stoll (1929) were amongst the earliest authors who successfully managed to rear two *Leptocera* species

(Sphaeroceridae) in the laboratory, by using boiled sheep manure as rearing medium. Fredeen & Glen (1970) succeeded in maintaining a laboratory colony of *L. caenosa* for 60 generations without adding new flies from the field by using six different rearing media.

Several obstacles were encountered during the experimental procedures of these temperature studies in the laboratory and precautions had to be taken. First the fermentation that normally takes place inside fresh dung could influence the temperature of the dung and had to be eliminated. Larsen & Thomsen (1940) conducted a temperature experiment on different fly species and emphasized that the temperature inside the manure is not constant despite the constant temperature in the incubator. At high temperatures fermentation takes place inside the manure. These, together with the larval activities inside the dung, both tend to increase the temperature. To ensure that the temperatures remained constant inside the incubators, it was important to expose the manure to the various temperatures 24 hours before the start of the experiment, because fermentation is the most vigorous during the first 24 hours. According to Larsen & Thomsen (1940), these precautions will keep temperature fluctuations within 1 to 2°C.

It was observed that over a period of four to seven days, the top layer (1-2 centimetres) of dung was over-utilized. It turned to a light brown colour and was extremely moist probably due to larval excrement. Under these conditions rearing of sphaerocerid flies became less successful. Stirring the rearing medium very carefully every second day rectified this situation. Vermiculite was also added to the dung because it enhanced the efficiency of the rearing medium (Goodhue & Cantrel, 1958). It was found that if the newly emerged flies which developed from the dung medium were not removed from the containers, but allowed to oviposit on the same dung, the success rates were much lower than those that were removed and transferred to containers with fresh feedlot dung. It was therefore necessary to transfer all newly emerged flies to other containers with fresh

dung to ensure that the laboratory colonies remained healthy, especially through the drier winter months when flies were not readily available at the feedlot.

Coboldia fuscipes (Meigen) (Diptera: Scatopsidae) was accidentally introduced into the sphaerocerid colonies at one stage, causing the latter species to die out within a two-month period. It is not known whether the Scatopsidae are predators on the Sphaeroceridae immature stages. However, it was decided to include this species as a bio-control agent in biological control experiments (see Chapter 7). New colonies of Sphaeroceridae were successfully established again after this incident.

3.3.2 Development and survival of eggs

The development times for the eggs of both species were longer at 12°C than at any other temperature (Fig. 3.4) and hatching was delayed. At 12°C the egg development of *C. vagans* and *C. hirtula* were 15.5 ± 1.3 days and 15.0 ± 1.1 days respectively, while at 36°C, it was calculated at only one day for both species (Fig. 3.4). Between 12°C and 36°C, egg development times of both species decreased.

The thresholds of development of the eggs were calculated by plotting the reciprocal of development time (1/t) against temperature. These "development zeros" were estimated by calculating the interceptions of the regression lines with the temperature axis. A very good linear relationship was found to exist for both *C. vagans* ($r = 0.98$) (Fig. 3.5) and *C. hirtula* ($r = 0.92$) (Fig. 3.6). The threshold of development temperature was found to be 11.7°C and 11.9°C for *C. vagans* and *C. hirtula* respectively. No hatching occurred below these threshold temperatures or above 36°C.

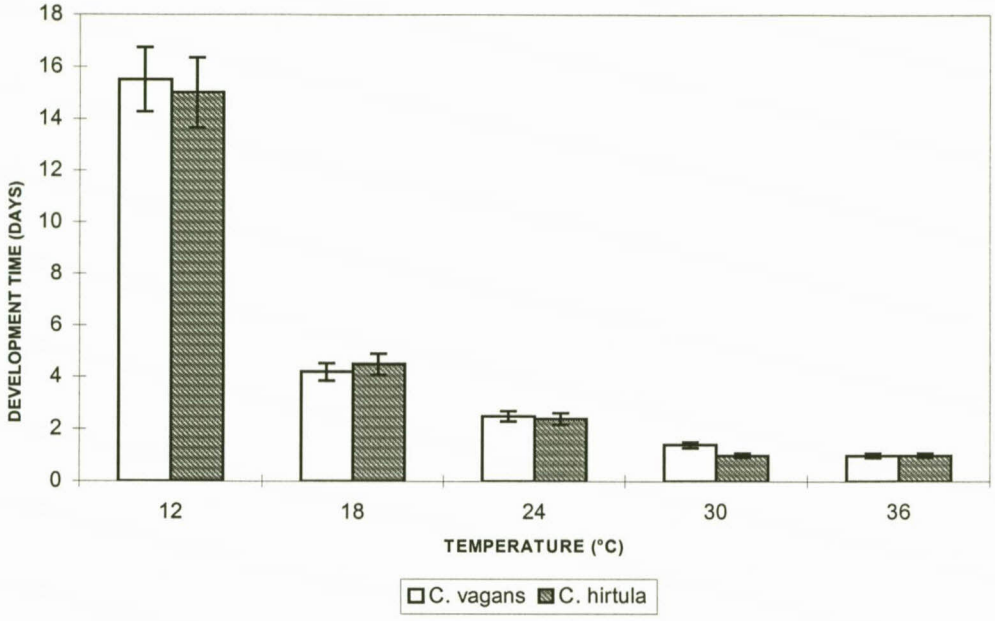


Figure 3.4: The development time of *Coproica vagans* and *Coproica hirtula* eggs at different constant temperatures.

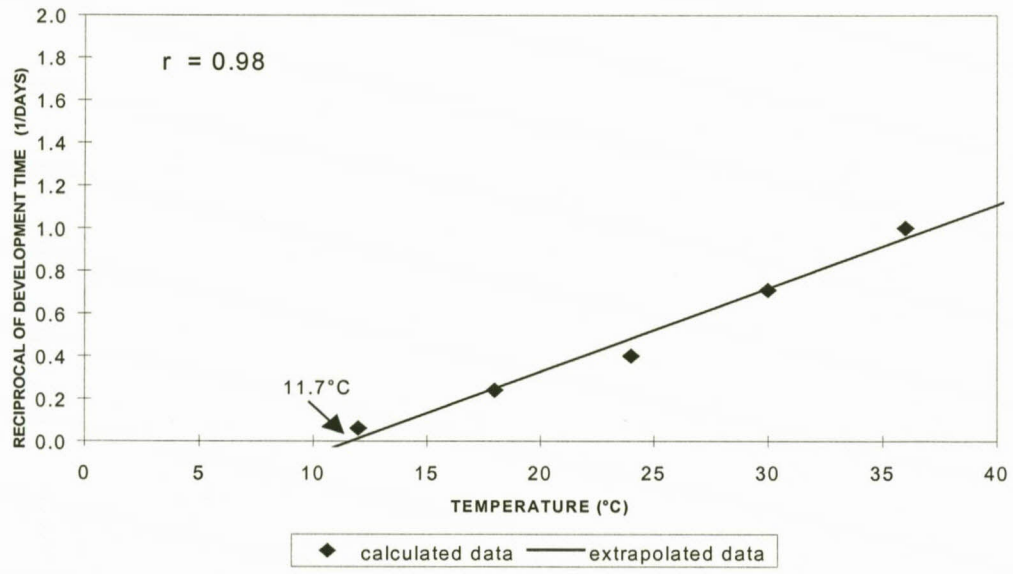


Fig. 3.5: The reciprocal of developmental time (1/days) of *Coproica vagans* eggs at different constant temperatures.

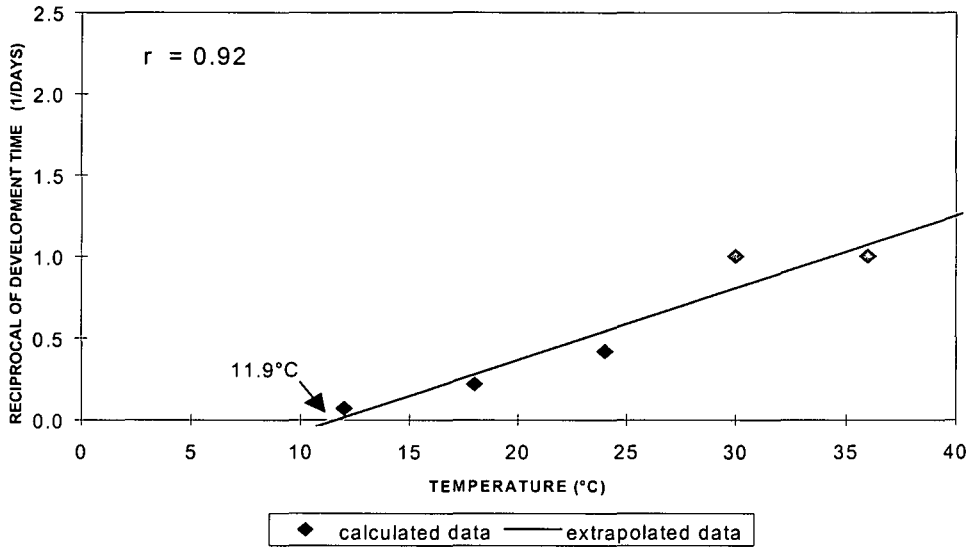


Figure 3.6: The reciprocal of development time (1/days) of *Coproica hirtula* eggs at different constant temperatures.

Analysis of variance ($F_{45;4}$=35.07) showed significant differences (P<0.05) in the duration of the egg stage of *C. vagans* exposed to the experimental temperatures (Table A3.1). Tukey's test ($Q_{0.05}$=11.50) indicated that egg development times at 12°C were significantly longer than those exposed to the other temperatures. At 18°C, the development times of the eggs were also significantly longer than at temperatures between 24°C and 36°C (Fig. A3.1). No significant difference was found in egg development between 30°C and 36°C (Fig. A3.1). Analysis of variance ($F_{45;4}$=49.63) also showed significant differences (P<0.05) in the duration of the egg stage of *C. hirtula* exposed to the different constant temperatures (Table A3.2). Tukey's test ($Q_{0.05}$=12.02) showed the same tendency as for *C. vagans* because the development rates of the two species were very similar (Fig. A3.2). This conclusion was given further support by applying a t-test designed for comparing the mean of two samples. It indicated no significant differences (P>0.05) between the development times of *C. vagans* and *C. hirtula* eggs at any of the temperatures where development times of the two species were compared (Table A3.17).

The highest hatching percentage of *C. vagans* eggs was 71.2 ± 8.8% at 24°C (Fig. 3.7). Above or below this temperature, hatching percentages decreased, although the rate was

slower at the higher temperatures (Fig. 3.7). For *C. hirtula*, the highest hatching percentage of the eggs was 58.9 ± 7.7% at 30°C and a decrease in hatching percentage was noted for all temperatures above or below 30°C. However, at 36°C the hatching percentage of 54 ± 6.8% was only slightly lower than at 30°C (Fig. 3.7).

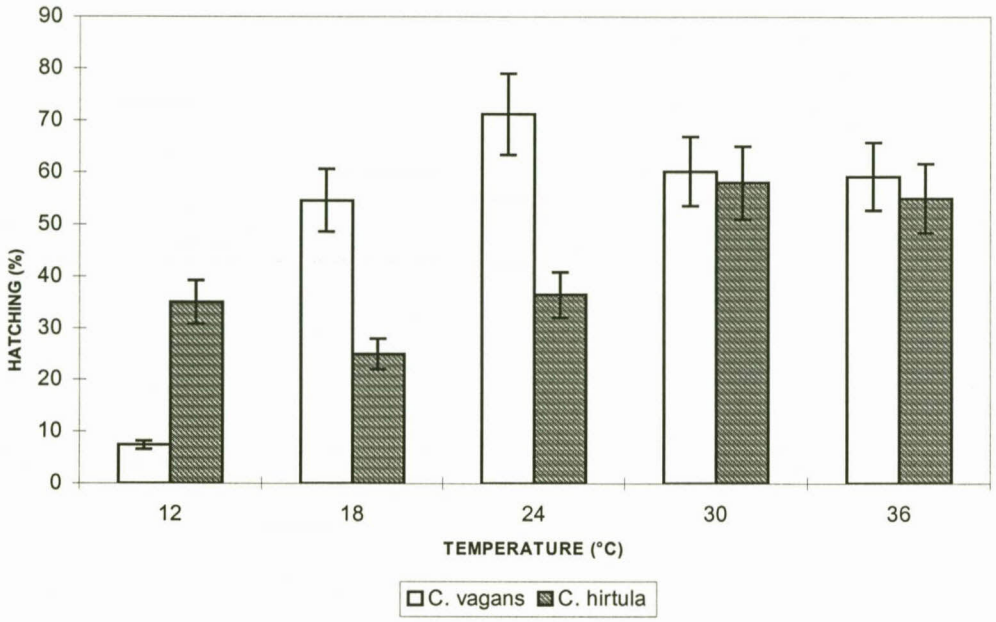


Figure 3.7: The hatching percentage of *Coproica vagans* and *Coproica hirtula* eggs at different constant temperatures.

Analysis of variance ($F_{45;4}$=41.03) showed that significant differences ($P<0.05$) occurred in the hatching of the eggs of *C. vagans* between the different constant temperatures (Table A3.3). Tukey's test ($Q_{0.05}$=12.33) indicated that the percentage egg survival of *C. vagans* at 12°C was significantly lower compared to those at temperatures of 18°C and above. Significant differences also occurred between 24°C and all the other temperature regimes for *C. vagans*, but between 30°C and 36°C, no significant difference was shown (Fig. A3.3). For *C. hirtula*, analysis of variance ($F_{45;4}$=14.88) also showed significant differences ($P<0.05$) in hatching percentage between the different constant temperatures (Table A3.4). Tukey's test ($Q_{0.05}$=6.75) indicated that the percentage survival of *C. hirtula* eggs at 30°C was significantly higher than all the other temperatures tested,

except at 36°C, where no significant difference was found between these two temperatures (Fig. A3.4). No significant difference in hatching was shown between 12°C and 24°C either (Fig. A3.4). With a t-test which compared the mean of two samples, significant differences ($P<0.05$) in hatching percentage were found between *C. vagans* and *C. hirtula* at all temperatures from 12°C to 36°C (Table A3.18). These statistical analysis indicated that *C. hirtula* eggs were more tolerant to low temperatures such as 12°C than *C. vagans* eggs, while the eggs of *C. vagans* showed higher hatching percentages at moderate temperatures (between 18 and 24°C) as well as at high temperatures (30 – 36°C).

These results showed that, within the limits of temperature tolerance, the development rate was significantly affected by temperature. At the warmer temperatures, 24°C - 36°C, the development time only varied between 1 and 2.5 days, indicating that the time required for egg development of both *C. vagans* and *C. hirtula* was short. These results are in accordance with findings by Hafez (1941), who stated that the duration of the egg stage of the sphaerocerid *C. ferruginata* in Egypt was also very short, about eight hours at 28°C. Hatching takes place the day after oviposition in *C. pedestris* (Sphaeroceridae) in Belgium (Guibè, 1939) and approximately 48 hours after ovipostion in *L. caenosa* (Sphaeroceridae) in Canada at 17°C (Fredeen & Taylor, 1964). As far as other fly species are concerned, Depner (1961) found that the duration of the egg stage of horn flies, *H. irritans*, in Alberta, Canada was 50 hours at 18°C, 22 hours at 24°C and 18 hours at 30°C. The duration of the egg stage of the buffalo fly, *L. exigua* (Muscidae), in Australia was 21 hours at 25°C and 15 hours at 35°C (Davidson, 1937). *Musca domestica* in Denmark spent just over nine hours in the eggs stage at 30°C (Larsen, 1943). The lesser house fly, *F. canicularis*, which is a serious pest on many poultry farms in Massachusetts and at 27°C, the development time for the eggs was 1.5 - 2 days (Steve, 1960).

The results furthermore showed that both low and high temperatures adversely affected egg hatching. It also indicated that 36°C was close to the upper development-hatching

threshold of the eggs. This hypothesis was supported by further tests in which none of the eggs hatched at 42°C. The embryological development of Sphaeroceridae eggs was most probably terminated at these temperatures extremes (below 12°C and above 36°C). The development thresholds, which is the lowest constant temperature at which both development and survival can be completed, were calculated for both *C. vagans* and *C. hirtula*. It seemed though as if the eggs of larger flies were more tolerant to lower temperatures compared to the eggs of smaller Sphaeroceridae. Feldman-Muhsam (1944) for instance, found that house fly eggs could survive lower temperatures if the exposure times were short, but even at -8°C, eggs still survived for an hour. This is consistent with the findings of Larsen & Thomsen (1940), who found that the eggs of *M. domestica* hatched at 10°C - 11°C in Denmark, but that severe larval mortality ensued. In Israel, house fly eggs showed a lower development rate at about 12°C, however, larvae were still able to develop at 8°C (Feldman-Muhsam, 1944). West (1951) indicated that house fly eggs failed to hatch at 11°C constant temperature in the laboratory. Richards (1958) designated the lowest temperature at which eggs hatch and the resultant larvae survive, as the "viability threshold". He demonstrated that loss in viability of insects at both low and high temperatures was the result of utilizing proportionally more energy in the development process (Richards, 1958).

Melvin (1934) on the other hand found that the eggs of *M. domestica* hatched at 43°C while those of *H. irritans* can hatch in temperatures of up to 60°C in the laboratory. In North Carolina, viability of eggs of *H. irritans* was also not affected by exposure to 48°C for 28 hours (Bruce, 1964). However, Sphaeroceridae eggs were not able to withstand such high temperatures. At temperatures above 36°C, no eggs survived. This could be attributed to the fact that the eggs of Sphaeroceridae are much smaller than those of *M domestica*, resulting in lower temperature tolerance and higher mortality rates. It could also be that the chorion of larger fly eggs is harder and thicker than those of smaller Sphaeroceridae eggs. The temperatures above the upper threshold could therefore not only affect the developing embryos, but also the physical properties of the chorion

(Karandinos & Axtell, 1967), rendering hatching of the smaller Sphaeroceridae eggs impossible.

The oviposition behaviour of Sphaeroceridae may also influence the effect of temperature on the development and survival of the eggs. Sphaeroceridae females lay their eggs either on the dung that serves as larval food, sometimes on the bottom or sides of small crevices or in tunnels made by dung beetles, with only the dorsal or antero-dorsal part uncovered, or on the surface of the soil, or on grass leaves or among stems under or near the larval food (Pitkin, 1989). This would imply that the eggs are confined to the surface of droppings most of the time. According to Hammer (1941), there is a vertical gradient of temperatures in a field dropping, with the largest changes and extremes in temperature just below the top surface of the dropping. Fly eggs are extremely susceptible to temperature extremes (Valiela, 1974), and it is therefore suspected that such temperature extremes and variations would be most important during the early development stages of sphaerocerid flies.

To comprehend the concept of threshold development of Sphaeroceridae, a detailed theory derived from the work of Hodson & Alrawy (1958) some discussion is necessary. These authors have shown that a variety of threshold effects may contribute to the following overall mortality of insects: (a) the temperature may be so low that no development occurs (= "development threshold"), (b) the temperature may be too low for development to reach completion (= "development-hatching threshold"). In this case, temperature may exert its effect by direct interference with development processes, or it may prolong the development period to such an extent that food reserves are depleted before development can be completed (Richards, 1958). (c) The embryo or pharate adult may have reached full development, but the temperature may be too low for the process of egg hatching or pupal emergence to be accomplished (= "hatching or emergence threshold"). Which of these three thresholds would be applicable to the two

sphaerocerids species remains difficult to say, although it is possible that all three may play a role in determining the individual development thresholds of eggs and pupae.

Messenger (1969) stated that the occurrence of different kinds of thresholds should be taken into account when the results of laboratory investigations are applied to natural populations. Thus, if an emergence threshold is involved, flies may fail to emerge when maintained at a given constant temperature, but this temperature would not be limiting in the field, where diurnal fluctuations about the mean would allow hatching at favourable times of the day (Messenger, 1969).

Another threshold effect has been reported Hodson & Alrawy (1958), namely the "hatching-survival threshold". They showed that incubation of eggs of some insect species at 17°C and 30°C permits successful completion of embryonic development, but that very few of the larvae survived to produce adults, despite their maintenance at under optimal conditions after hatching. In this case the lethal effects of temperatures are not manifested until the later stages of development have been reached (Hodson & Alrawy, 1958). If such latent effects should prove to be generally characteristic of insects, they would seriously limit the applicability of much laboratory data on development thresholds (Messenger, 1969). However, this phenomenon was not a serious concern for the spherocerid species, since immature survival proved to be good at the optimal constant temperature conditions under which the laboratory colonies were kept.

3.3.3 Development and survival of larvae

Similar to the egg stages, the total development time for the larvae increased with a decrease in temperature (Fig. 3.8). At 12°C, development times were 27.2 ± 1.5 days and 27.5 ± 1.5 days for *C. vagans* and *C. hirtula* respectively, while at 36°C it was 2.5 ± 0.2 days for both species (Fig. 3.8). At 6°C, no hatching or larval development took place, while at 12°C, the survival of *C. vagans* larvae was poor, and the majority had failed to

progress beyond the first instar. However, the survival of *C. hirtula* larvae at cooler temperatures such as 12°C and 18°C was significantly better than *C. vagans*.

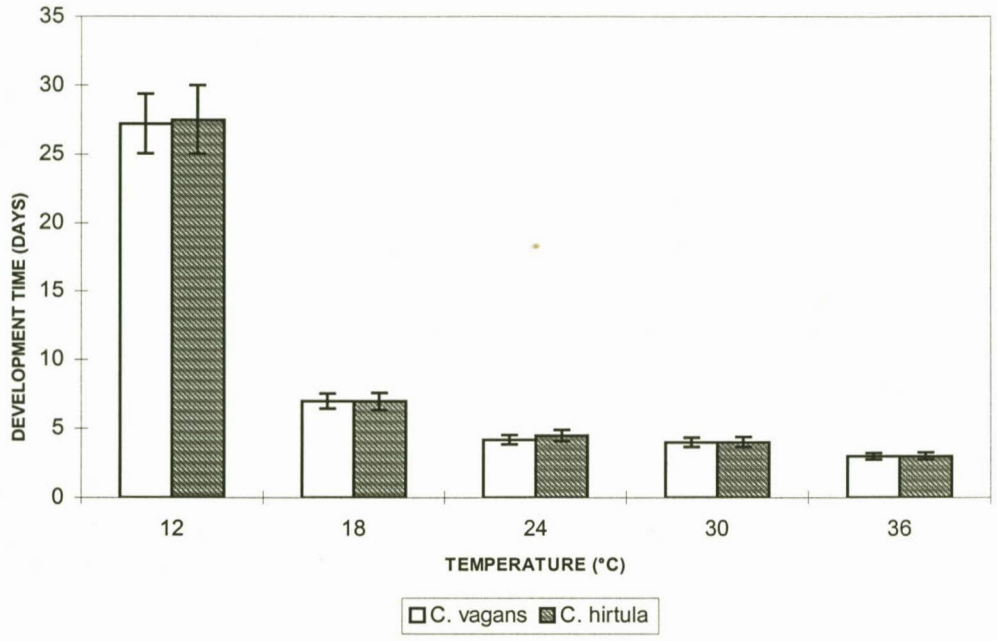


Figure 3.8: The development time of *Coproica vagans* and *Coproica hirtula* larvae at different constant temperatures.

The threshold temperature for larval development (1/days) of *C. vagans* and *C. hirtula* was determined by plotting the reciprocal of development time against temperature and then extrapolating the data (Figs 3.9 & 3.10). A linear relationship was found for both species (r = 0.95 and 0.97 respectively), and development thresholds were calculated at 6.3°C and 6.7°C respectively (Figs 3.9 & 3.10).

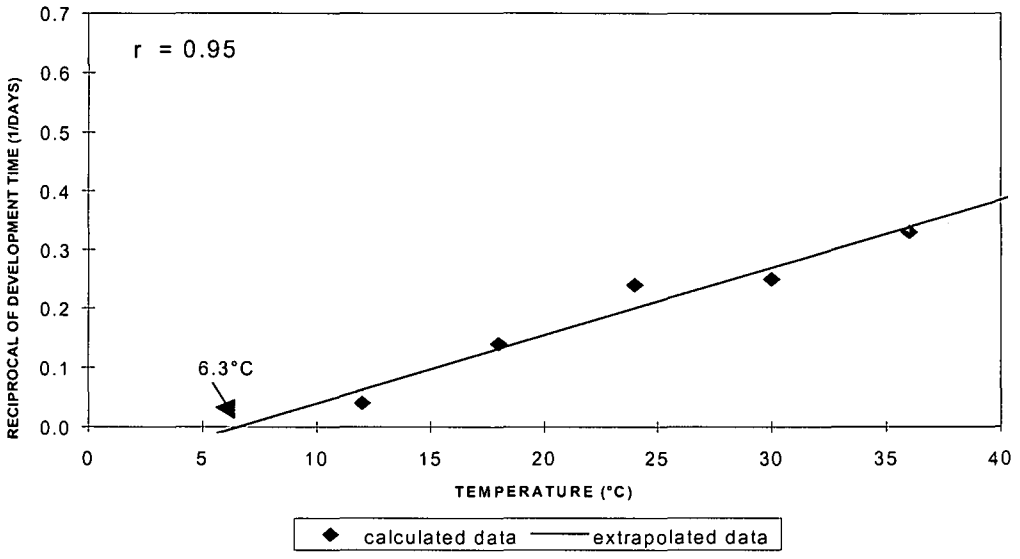


Figure 3.9: The reciprocal of development time (1/days) of *Coproica vagans* larvae at different constant temperatures.

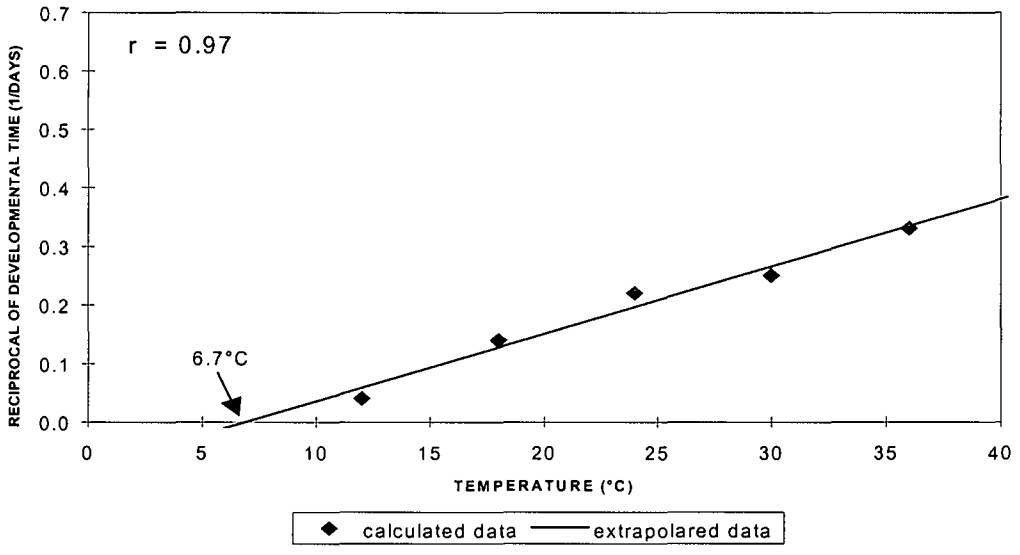


Figure 3.10: The reciprocal of development time (1/days) of *Coproica hirtula* larvae at different constant temperatures.

Based on analysis of variance ($F_{70;4}$=56.85), significant differences (P<0.05) were shown to exist between the larval development times of *C. vagans* (Table A3.5). Tukey's test

($Q_{0.05}$=31.81) showed that significant differences existed in the development times of *C. vagans* larvae between 12°C, 18°C and 24°C (Fig. A3.5). The differences in development times between 24°C, 30°C and 36°C were not significant. Analysis of variance ($F_{70;4}$=80.12) also showed significant differences (P<0.05) in the larval development times between the different constant temperatures for *C. hirtula* (Table A3.6). With Tukey's test ($Q_{0.05}$=33.93), the same significant differences occurred as for *C. vagans* (Fig. A3.6). In comparing the development times of the two species with each other, a t-test was used. This statistical test showed that no significant differences (P>0.05) existed between the two species at any of the temperature intervals which were tested (Table A3.17).

Survival of *C. vagans* and *C. hirtula* larvae was the highest at 24°C *viz.* 67 ± 6.8% and 66 ± 6.7% respectively, decreasing above or below this temperature (Fig. 3.11). At extreme temperatures (below 6°C and above 36°C), larval survival rates were zero and are therefore not indicated in any of the figures.

Analysis of variance ($F_{70;4}$=26.25) showed significant differences (P<0.05) in the larval survival of *C. vagans* between the different temperatures (Table A3.7). Tukey's test ($Q_{0.05}$=11.00) showed that survival of *C. vagans* larvae at 12°C, 18°C and 36°C were significantly lower (P<0.05) than those between 24°C and 30°C, although no significant differences in survival occurred between 24°C and 30°C (Fig. A3.7). However, for *C. hirtula*, analysis of variance ($F_{70;4}$=0.49) showed no significant differences (P>0.05) between the various temperatures that were tested (Table A3.8 & Fig. A3.8). A t-test was used to compare the larval survival rates of the two species with each other. Significant differences (P<0.05) were shown between the larvae of *C. vagans* and *C. hirtula* at all the temperatures except 24°C (Table A3.18). This clearly shows that the larval survival of both species was equally good at optimum temperature conditions (24°C). Furthermore these results indicated that *C. hirtula* larvae were more temperature tolerant

than *C. vagans*, and would probably be capable of surviving at lower environmental temperatures.

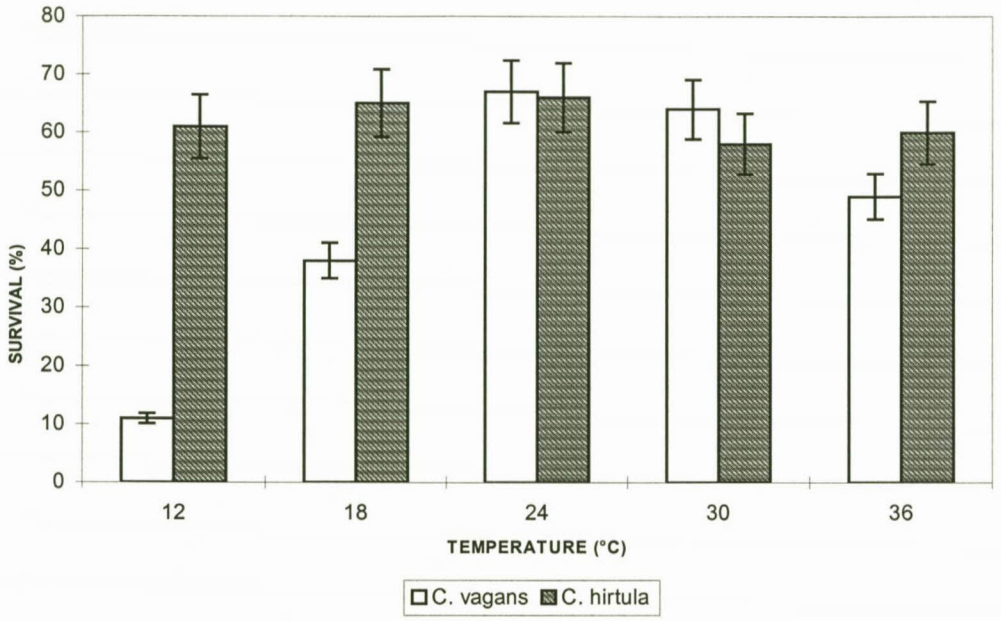


Figure 3.11: Percentage survival of *Coproica vagans* and *Coproica hirtula* larvae at different constant temperatures.

Literature on the effect of temperature on duration of development of *C. vagans* and *C. hirtula* larvae is scarce and this study provided new information on the adaptation of these species to a range of temperatures. The duration of the larval stages was longer than the egg stages for both *C. vagans* and *C. hirtula*. This corresponds with the findings of Guibè (1939) who showed that larvae of *C. pedestris* pupated nine days after oviposition. Hafez (1949) found that the larval duration of *C. ferruginata* in Egypt was 3-4 days at 28°C, while in Canada larval duration of *L. caenosa* was 9-15 days after oviposition at 17°C (Fredeen & Taylor, 1964). Many studies involving the effect of temperature on fly species other than Sphaeroceridae have been conducted. Greenham (1971) found that the effect of temperature on the rate of development of bushfly larvae in cattle dung in Australia was approximately linear from the threshold temperature of 12°C up to 39°C. The same linear effect was also reported for *Sarcophaga*

(*Parasarcophaga*) *misera* (Fallèn) between 15°C and 40°C by Parashar *et al.* (1997) in India and also for *Parasarcophaga* (*Liopygia*) *ruficornis* (Fallèn) between 13°C and 37°C by Amoundi *et al.* (1994). Chen *et al.* (1987) showed that a linear relationship existed between development and temperature for *S. crassirostris* within the range of 15 - 30°C. The current results furthermore showed an increase in development times of Sphaeroceridae larvae as temperatures decreased, which is in agreement with the findings of Depner (1961), who stated that the duration of the larval stage of horn flies in Canada was 10.5 days at 18°C, 5.6 days at 24°C and 3.7 days at 30°C. The larval stage of the buffalo fly, *L. exigua,* in Australia was 5.9 days at 25°C and 4.9 days at 35°C (Davidson, 1937). In New England, USA, the larval stage of the lesser house fly, *F. canicularis*, lasted for 8-10 days at 20°C (Steve, 1960). These differences in development duration cannot only be attributed to the response of different fly species to a certain temperature range. Vargas *et al.* (1996) suggested those differences at certain individual temperatures between the present and previous studies may also be as a result of differences in test diets, rearing procedures, or laboratory adaptations of test strains used in the different studies.

Results of the current study on larval survival of Sphaeroceridae indicated that low temperatures are effective parameters in lowering the survival rate of Sphaeroceridae larvae at the extremes of this particular temperature range. This was consistent with a previous temperature study conducted by Feldman-Muhsam (1944), who investigated the temperature effect on many dipteran larvae in Egypt and found that house fly larvae all died at -4°C. West (1951) showed that all instars of house fly larvae survived at 0°C in the laboratory, although they did not undergo any further development. Their movements also slowed down and they congregated at the centre of the medium (West, 1951). Below 12°C, larval development of the Sphaeroceridae did not continue, although the theoretical threshold temperature for larval development was calculated at 6.3°C and 6.7°C for *C. vagans* and *C. hirtula* respectively. These development thresholds for the larval stage were unexpectedly low for both species, which probably reflects some

biological influence. Regarding this, development thresholds for larvae may have been influenced by a behavioural trait of the cohorts (Vargas *et al.*, 1996). It was observed that at cool temperatures, larvae aggregated at the bottom of the small containers, probably to stay warm. Karandinos & Axtell (1967) showed that some development could take place at temperature levels lower than the development zero. It has therefore been suggested by Karandinos & Axtell (1967) that development zeros should rather be considered as those temperatures where biological material such as eggs or pupae can be maintained for maximum time without completing their hatching or development and without being killed. It is well known that over a broad range of temperatures, the relationship between temperature and rate of development is sigmoid rather than linear (Karandinos & Axtell, 1967). Nevertheless, over the medial portion of this particular temperature range, the assumption of a linear model adequately describes this phenomenon and provides a simple and useful tool for estimations of the development thresholds.

Results from the current study showed that 24°C was the most suitable temperature for both sphaerocerid species in terms of the percentage of larvae successfully maturing and of the number of larvae pupating. This does not correspond with the findings by West (1951) who found that the optimum development temperature for house fly larvae in the laboratory was between 35°C and 40°C, which could be attributed to the fact that larger flies probably have higher optimum development temperatures than the smaller Sphaeroceridae. During these experiments the survival of the larval stage was examined and no distinction was made between the three instars. However, it could be expected that certain instars are more susceptible to extreme temperatures than others. Bruce (1964) who studied the horn fly *H. irritans* in the USA found that the third instar larvae were more resistant to low temperatures than the earlier stages, whilst Hafez (1941) found that the first instar in the Egyptian fly, *Musca vicina* Macquart, was the most sensitive to high temperatures. In Denmark, Larsen (1943) showed, in a series of experiments, that for any length of exposure time, first instar larvae of *M. domestica* were more vulnerable to high temperatures than the other larval instars, although not as

sensitive as the eggs. There was probably more variation in house fly tolerance, since larvae of the tropical subspecies, *M. domestica corrina*, in tropical areas of central Africa may survive exposure at 60°C for up to an hour (Roubaud, 1916).

Although the survival rates of larvae were not tested at temperatures above 36°C, it was noted that when the larval medium became too hot, the larvae left the medium and accumulated on the sides of the glass vials where they eventually died. However, this could also be attributed to the dung medium becoming drier as the temperature increased. In field droppings these larvae would probably have migrated to cooler sections of the pat to escape the effect of the heat, although no such observations were made. In Denmark, Larsen & Thomsen (1940) found in field studies conducted with *Stomoxys calcitrans* (Linnaeus), *M. domestica* and *H. irritans* that the percentage larval survival was considerably reduced at lower temperatures. In the latter case the exposure of larvae to various other mortality factors such as predation, parasitism, competition and starvation are therefore prolonged, provided these predators and other organisms are adapted to tolerate these low temperatures (Larsen & Thomsen 1940). Hammer (1941) and Valiela (1974) furthermore suggested that first instar larvae are very susceptible to these extreme temperatures, because they are limited to the top part of dropping. Should the temperature become unfavourable at the top of the droppings, mature larvae can move down to a more favourable part of the dung pats, since they are then very active, capable burrowers (Valiela, 1974). In addition, Larsen & Thomsen (1940) stated that the mortality rate for larvae might be so high due to the fact that at low temperatures certain essential food substances in the rearing medium are not formed at all, or not available in sufficient quantities. It could also be that due to these very low temperatures, Sphaeroceridae larvae do not have enough energy to feed at a required rate because of a very slow metabolism, as was suggested by Karandinos & Axtell (1967). As a result of that, food consumption might be too low to sustain life and the larvae would therefore die of starvation.

3.3.4 Development and survival of pupae

Pupal development times also decreased with an increase in temperature (Fig. 3.12). At 12°C the development times were 35 ± 2.1 days and 37 ± 2.6 days for *C. vagans* and *C. hirtula* respectively, while at 36°C, the development times were only 4.0 ± 0.25 days for both species (Fig. 3.12). The threshold temperature for pupal development (1/days) of *C. vagans* and *C. hirtula* was determined by plotting the reciprocal of development time against temperature and then extrapolating the data. The line showed a linear relationship for both species (r = 0.92 and r = 0.93 respectively), and development thresholds were calculated at 7.6°C and 8.2°C respectively (Figs 3.13 & 3.14).

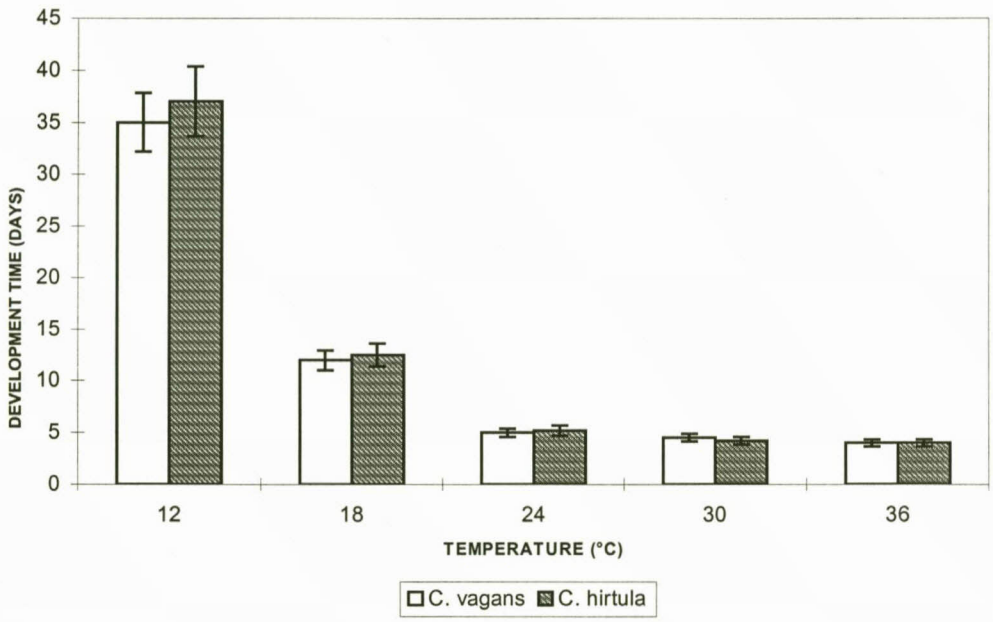


Figure 3.12: The development time of *Coproica vagans* and *Coproica hirtula* pupae at different constant temperatures.

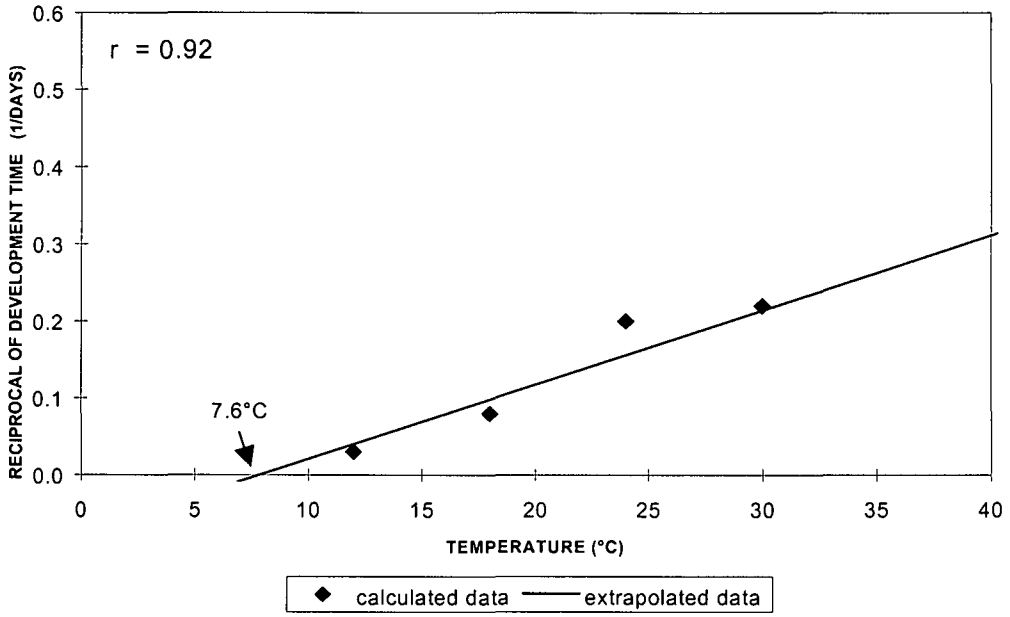


Figure 3.13: The reciprocal of development time (1/days) of *Coproica vagans* pupae at different constant temperatures.

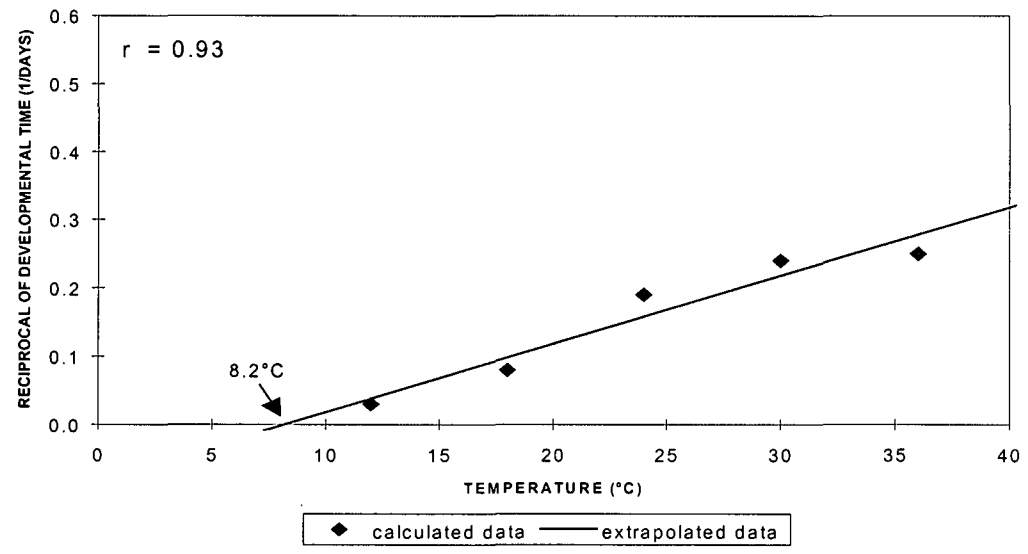


Figure 3.14: The reciprocal of development time (1/days) of *Coproica hirtula* pupae at different constant temperatures.

In the case of *C. vagans*, the highest survival percentage for the pupae was at 24°C (Fig. 3.15), which was similar to both the eggs (Fig. 3.7) and larvae (Fig. 3.11). However, for *C. hirtula* the highest pupal survival occurred at 30°C (Fig. 3.15), which clearly indicated that *C. hirtula* pupae had a higher upper temperature threshold than *C. vagans*. At temperatures above and below these optimum levels (24°C and 30°C respectively), pupal survival of both species decreased (Fig. 3.15). An important observation is the very high survival rates for the pupae of both species (82.5 ± 7% and 88.5 ± 8% respectively) in comparison to the eggs and the larvae (Figs 3.7 and 3.11).

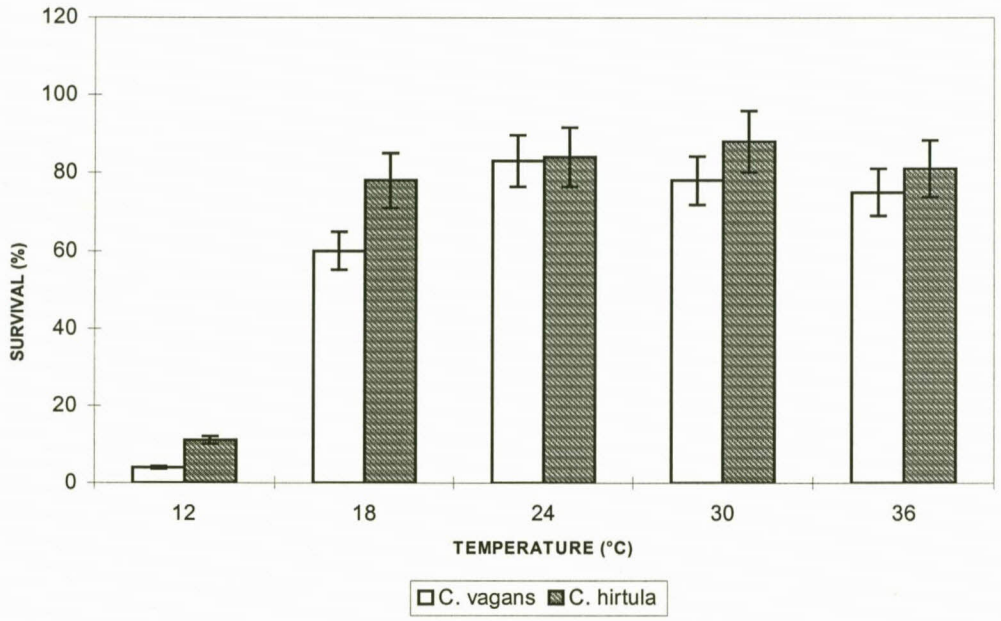


Figure 3.15: Percentage survival of *Coproica vagans* and *Coproica hirtula* pupae at different constant temperatures.

Analysis of variance ($F_{55;4}$=26.26) showed significant difference (P<0.05) in survival of the *C. vagans* pupae (Table A3.11), while Tukey's test ($Q_{0.05}$=9.66) indicated that pupal survival at 24°C was significantly better than those at all the other temperatures tested, and no significant difference was recorded between 30°C and 36°C (Fig. A3.11). For *C. hirtula*, significant differences (P<0.05) were also shown with analysis of variance ($F_{55;4}$=37.26) (Table A3.12). Tukey's test ($Q_{0.05}$=16.13) showed that the percentage pupal

survival at 30°C was significantly higher compared to the rest of the temperature regimes, except at 24°C (Fig. A3.12). No significant differences were found between 18°C, 24°C and 36°C. Survival of the pupae at 12°C was also significantly lower than the survival at 18°C and above (Fig. A3.12). A t-test was again used to compare the mean pupal survival of *C. vagans* and *C. hirtula* with each other. Significant differences ($P<0.05$) were shown between the pupae of both species at all the temperatures except 24°C (Table A3.18). Pupal survival of *C. hirtula* was significantly better than those of *C. vagans* at almost all temperatures, supporting the view expressed earlier that *C. hirtula* pupae had a higher upper temperature threshold.

The duration of the pupal stages was longer than the egg stages or the larval stages for both Sphaeroceridae species. However, this does not correspond with the findings of Hafez (1941) who studied the life history of *C. ferruginata* in Egypt and found that the pupal stage was about two days at 28°C, and thus shorter than the larval stage. The results from the current study do agree with other findings though, such as those of Guibè (1939) who found that in *C. pedestris* the adults emerged 10 days after pupation at 20°C in Belgium. In Canada, the pupal stage of *L. caenosa* generally lasted 7-8 days, and sometimes even as long as 11 days at 17°C (Fredeen & Taylor, 1964). In Britain, adults of *Herniosina bequaerti* (Villeneuve) (Sphaeroceridae) emerged 16-18 days after pupation at 15°C (Goddard, 1938). These findings are also in agreement with those of Davidson (1937) who stated that the pupal development time of the buffalo fly, *L. exigua*, in Australia was 6.5 days at 25°C and 4.8 days at 35°C. Depner (1961) found that the duration of the pupal stage of horn flies in Canada was 13.5 days at 18°C, 7.1 days at 24°C and 4.9 days at 30°C. The duration of the pupal stage of *F. canicularis* in New England was calculated to be between 9 and 10 days (Steve, 1960). An important aspect of all these studies is that most were conducted in the Northern Hemisphere, and careful consideration should therefore be given when results are compared. The response of Sphaeroceridae flies and their immature stages to different constant temperatures will

most probably be slightly different from those studies that were conducted elsewhere because of an acclimation factor of the different species to their environments.

The survival of pupae was high in comparison to the other stages in the life cycle of the two sphaerocerid species investigated in the current study. Even extreme temperatures that seemed conducive to pupal survival (such as 12°C and 36°C), they still survived, although they appeared visibly smaller than pupae kept at the milder temperatures such as 24°C and 30°C. These findings are in accordance with those of Depner (1961) who found that in studies done on horn flies in Alberta (Canada), temperatures approaching the lower development threshold resulted in the formation of small, very transparent puparia. This in turn resulted in the production of small adults that, in some cases, were only half the normal size (Depner, 1961). Horn flies hibernate in Canada either as mature larvae or as puparia, with the latter as the most common (McLintock & Depner, 1954). West (1951) mentioned that pupation of house flies in the laboratory takes place at lower temperatures than those favoured by the larvae. This may partially explain the migration of the full-grown larvae to the glass walls of the vials. However, the effect of moisture will undoubtedly also be an additional factor here, since pupation normally takes place at drier places in the dung pat (Valiela, 1974). It thus seems as if the eggs were generally more sensitive to abnormally high temperatures than the larvae, which in turn were more sensitive than the pupae.

3.3.5 Total duration of development

For *C. vagans*, the minimum development time occurred at 36°C. Despite the very high mortality rates at this temperature, the duration of the immature life from oviposition to adult emergence was 8.0 ± 0.7 days, compared to 12°C where the total development time was 81 ± 7.7 days. For *C. vagans*, where the optimum development was at 24°C (see Figs. 3.7, 3.11 and 3.15), the total development time was 12 ± 0.9 days, and it became progressively longer as the temperature decreased (Fig. 3.16). The threshold of

development (1/t) for *C. vagans* was calculated by plotting the reciprocal of development time against temperature (r = 0.89) and was found to be 8.8°C (Fig. 3.16).

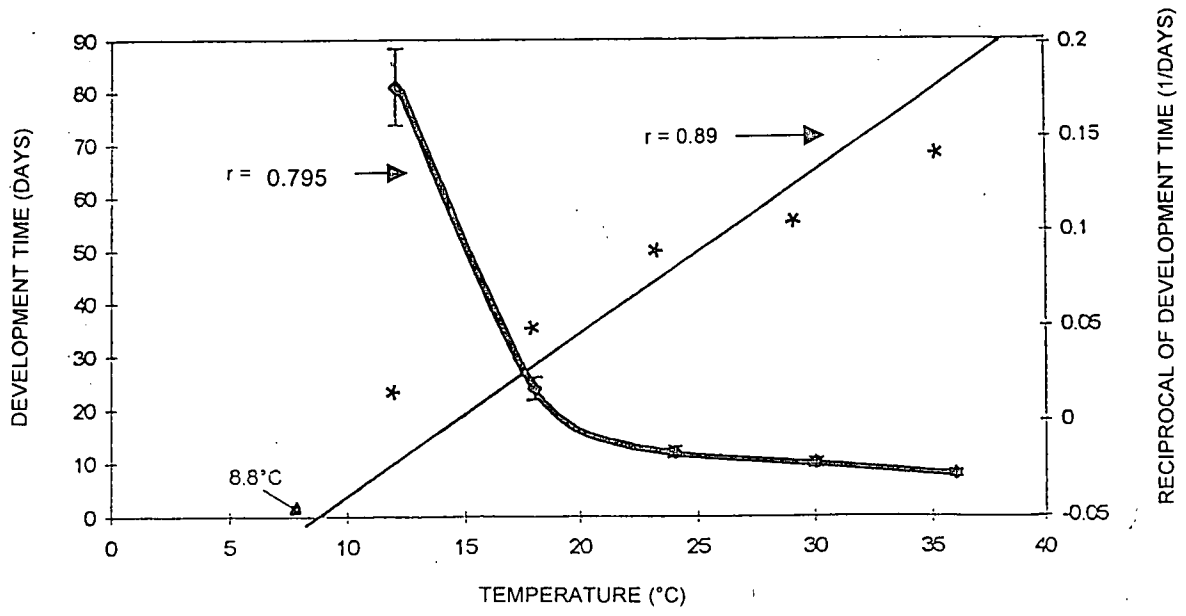


Figure 3.16: Total development time and reciprocal of development time of *Coproica vagans* at different constant temperatures.

The minimum development time for *C. hirtula* was also 36°C. Despite the very high mortality that also occurred at this temperature, the life cycle (from egg to adult) was completed in only 7.7 ± 0.65 days, compared to 12°C where the total development time was 82 ± 7.9 days (Fig. 3.17). In the case of *C. hirtula*, the optimum development temperature was 30°C (Figs. 3.7, 3.11 and 3.15) and the development time at 30°C was approximately 10 ± 0.85 days (Fig. 3.17). The threshold of development (r = 0.87) was 9.2°C (Fig. 3.17).

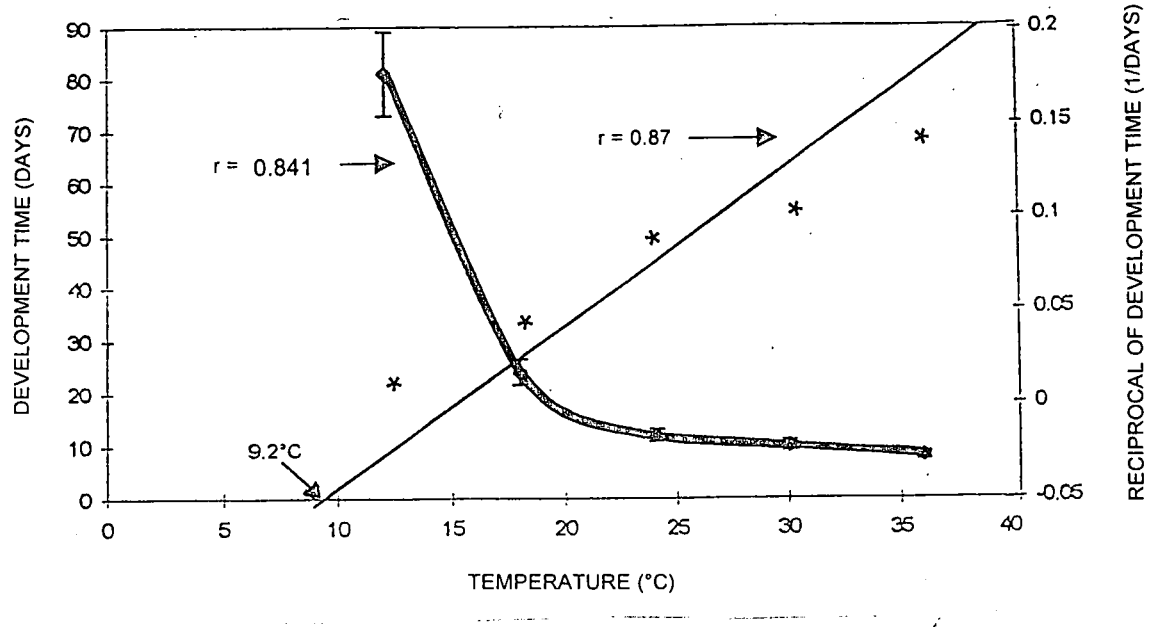


Figure 3.17: Total development time and reciprocal of development time of *Coproica hirtula* at different constant temperatures .

Many other studies had been done in which the total development rate of flies at different constant temperatures was investigated (Thomsen & Hammer, 1936; Davidson, 1937; Depner 1961 and Fredeen & Taylor, 1964). Results generally showed a clear trend of longer development at lower temperatures accompanied by lower survival at both lower and higher temperatures. The growth period of the immature stages of *C. vagans* and *C. hirtula* decreased from over 80 days to 8 days as dung temperatures increased from 12°C to 36°C. This is consistent with previous life table studies for other fly species conducted at moderate temperatures. Thomsen & Hammer (1936) found that in the case of *Sphaerocera subsultans* (Meigen) in Denmark, the minimum total duration of development at 18°C - 20°C was 14 - 15 days, and at 23°C - 24°C, it was 13 days. Thomsen & Hammer (1936) also found that *Limosina* sp. had a minimum total duration of development of only 13 days. They furthermore calculated the total duration of development for several other dipteran species in Denmark and produced the following

results: 13 days for *Muscina stabulans* (Fallèn) (Muscidae) at 31°C; 20 days for *Morellia hortorum* (Fallèn) (Muscidae) at 19°C; 21 days for *F. canicularis* at 22°C and 13 days for *Sepsis* sp. (Sepsidae) at 24°C (Thomsen & Hammer, 1936). According to Davidson (1937), the total development times of the buffalo fly, *L. exigua*, in Australia were 13.5 days at 25°C and 10.4 days at 35°C. Amoundi *et al.* (1994) reported a minimum developmental period at 34°C (15 days) and maximum at 16°C (48.6 days) for *P.ruficornis*, exhibiting a linear correlation between 16°C and 34°C.

The fact that rate of development is highest at a particular temperature does not mean that the rate of emergence will be highest at that temperature (Lee & Denlinger, 1985b). This hypothesis was supported by observations on Sphaeroceridae during these experiments, and it was noted that at 36°C, the total development times of the sphaerocerid flies were very short, but the mortality was very high (between 72% and 81%). Lee & Denlinger (1985b) also stated that an increase in mortality near the lower critical limit would enhance the effect of temperature on development rate in depressing emergence rates. When the relationship between temperature and the reciprocal of development duration is reviewed, a linear regression line is obtained. This is of importance in relation to doubts that have been expressed concerning the use of constant temperatures in experiments designed to establish the velocity of development. Harries (1943) found that the rate of development under conditions of fluctuating temperatures appeared to diverge widely from that which characterized the same average constant temperatures. The situation is complicated by the fact that sometimes fluctuating temperatures appear to cause a retardation of development and sometimes it causes an acceleration (Clarke, 1967), or sometimes it has no effect on the development at all (Wardhaugh *et al.*, 1969). The effect of fluctuating environmental temperatures on the Sphaeroceridae will be dealt with later in more detail.

Using the data which was obtained during these experiments, coupled with the average dung temperature during the summer in the Free State, the expected number of

generations of Sphaeroceridae could be as high as four in just over a month (32 days), should conditions at the feedlot remain favourable. The portion of total development period that was spent in each of the development stages did not differ much between the two Sphaeroceridae species. The egg stage of *C. vagans* required 21.7% of the total time, the larval stage 34.8% and the pupal stage 43.5%. In the case of *C. hirtula*, the percentage of the total time that the eggs, larvae and pupae required was 18.6%, 38.1% and 43.3% respectively. The portion of the total development period, which was spent in each of the development stages, did not remain constant when temperatures changed. When temperatures were lowered, the egg and pupal portions decreased, but the larval portion increased. This phenomenon indicates that the active larval stage is more dependent on the environment for its development than the inactive egg or pupal stages.

In general, insect development can only occur within a fairly narrow range of temperatures and the development thresholds have been determined for a number of insects at different stages of development. For these two Sphaeroceridae species in particular, the development thresholds seemed to be between 12°C and 36°C. This more or less corresponds with the findings of Bar-Zeev (1959), who found that in the case of *Aedes*, which has a particularly narrow range like the Sphaeroceridae, the lower temperature limit was 14°C and the upper limit 36°C.

3.3.6 Production and life expectancy of adult flies

For *C. vagans*, a highest average of 35 ± 2.5% of all eggs developed to adulthood at 24°C. At 12°C, this figure was as low as 0.1% compared to 24 ± 1.9% at 30°C and 22 ± 1.7% at 36°C. (Fig. 3.18). In the case of *C. hirtula*, a highest average of 29.8 ± 1.8% of all eggs produced developed into adult flies at 30°C (Fig. 3.18). At 12°C, only 1.7 ± 0.3% of the eggs developed into adult flies, which is slightly higher than that of *C. vagans*.

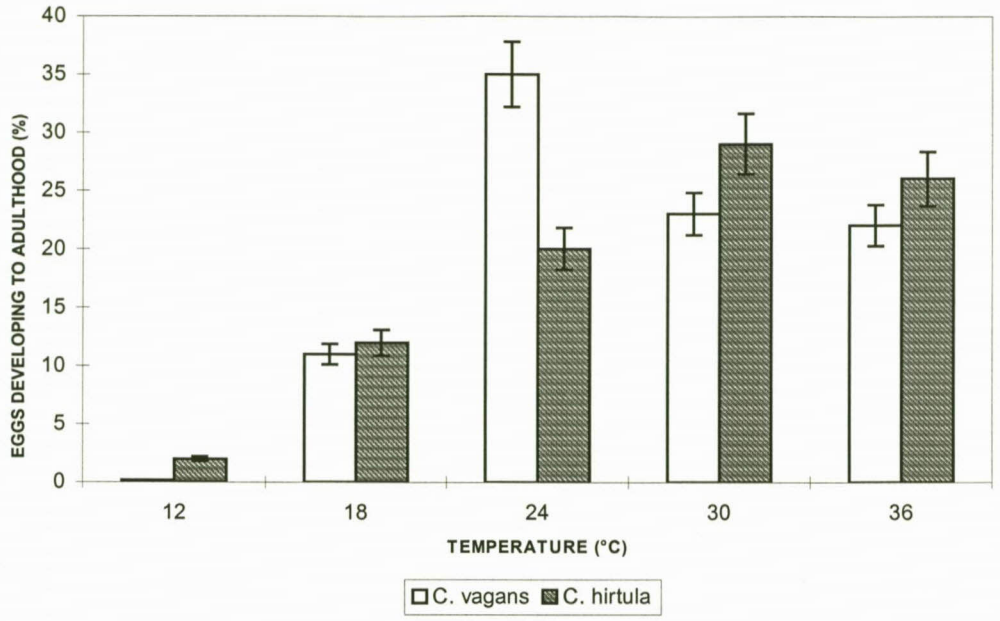


Figure 3.18: Percentage of *Coproica vagans* and *Coproica hirtula* eggs developing to adulthood at different constant temperatures.

Based on analysis of variance ($F_{70;4}$=14.62), significant differences were shown (P<0.05) in adult emergence of *C. vagans* (Table A3.13). Tukey's test ($Q_{0.05}$=8.99) showed that fly emergence at 12°C, 18°C and 24°C differed significantly from one another and also from the other temperature regimes tested (Fig. A3.13). No significant difference in adult emergence was shown between 30°C and 36°C. For *C. hirtula*, analysis of variance ($F_{70;4}$=34.68) also showed significant differences (P<0.05) in the production of adults (Table A3.14). Tukey's test ($Q_{0.05}$=19.68) showed significant differences between all the different temperature regimes, except between those values at 30°C and 36°C (Fig.A3.14). To compare the two species, a t-test was performed. Significant differences (P<0.05) in the percentage eggs that reached adulthood were shown between *C. vagans* and *C. hirtula* at all temperatures tested except at 18°C. (Table A3.19).

For both species, the life expectancy of the adult flies increased as the temperature decreased between 36°C and 12°C. At 12°C, adult flies survived up to 40 ± 4.3 days for *C. vagans* and 44 ± 4.4 days for *C. hirtula*. At 36°C the adults survived for approximately 9.0 ± 0.8 days for *C. vagans* and 6.0 ± 0.7 days for *C. hirtula* (Fig. 3.19).

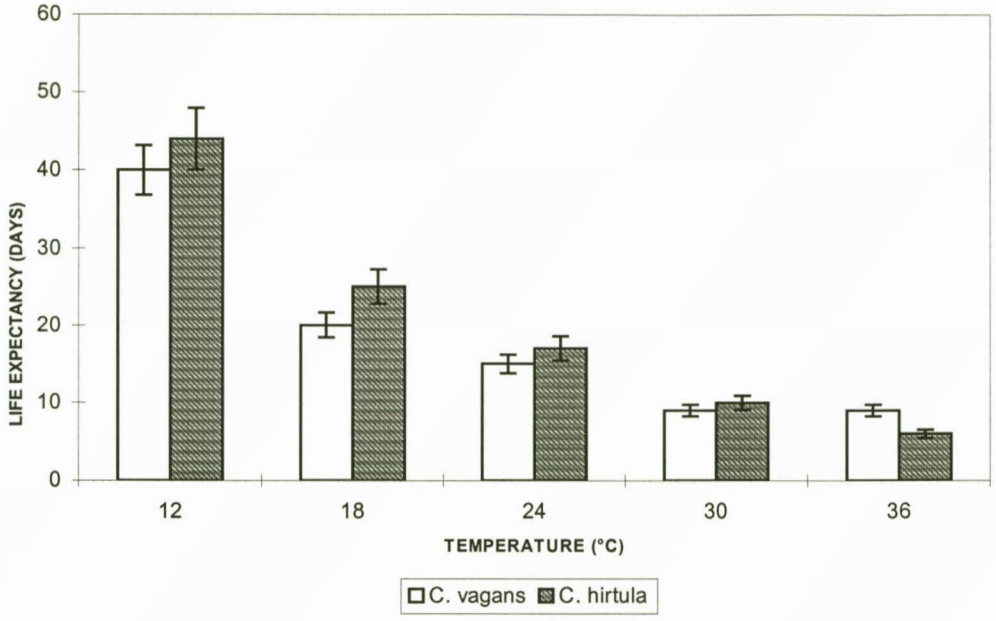


Figure 3.19: The life expectancy of the adult *Coproica vagans* and *Coproica hirtula* at different constant temperatures.

Analysis of variance ($F_{45;4}$=25.54) showed that significant differences (P<0.05) existed in the life expectancy of *C. vagans* (Table A3.15), while Tukey's test ($Q_{0.05}$=8.39) showed that the life expectancies of the flies at 12°C were significantly longer compared to those at the other temperature regimes (Fig. A3.15). The same effect was also shown for the life expectancies at 18°C and 24°C. However, there were no significant differences in life expectancy between 30°C and 36°C. For *C. hirtula* significant differences (P<0.05) were also shown in the life expectancy of the adult flies with analysis of variance ($F_{45;4}$=34.18) (Table A3.16). Tukey's test ($Q_{0.05}$=14.62) indicated that significant differences existed in life expectancies at all temperatures from 12°C to 36°C (Fig. A3.16). By applying a t-test to the results, significant differences (P<0.05) between the life expectancies of *C. vagans* and *C. hirtula* adults were shown at all temperatures tested except at 30°C (Table A3.19). This indicates that hot conditions in summer at the feedlot will not influence one species significantly more than the other. However, at very high temperatures such as 36°C, significant differences between the two species were shown again, proving that these high temperatures above 30°C favoured *C. vagans* adults.

Adult Sphaeroceridae are present at feedlots mainly during warmer periods of the year from October to March, when temperatures can be expected to be between 12°C and 36°C for most of the time. The results indicated that life expectancies of adult sphaerocerids were between 10 and 25 days at temperatures ranging from 18°C to 30°C. It can therefore be expected that proliferation of sphaerocerids during these periods will be extremely high because of the longevity of adult flies and also because of their fecundity. These results are in agreement with the findings of Davidson (1937) who stated that places in Australia which have monthly mean temperatures of 20°C or less, may be placed outside the range of permanent occupation of the buffalo fly, *L. exigua* (Muscidae). In the case of *Anatalanta aptera* Eaton (Sphaeroceridae), physiological studies by Vernon & Vannier (1996) revealed an exceptional longevity (nine months at 5°C), due to special increased supercooling abilities by these flies. This indicates the possible absence of such a supercooling feature in *C. vagans* and *C. hirtula* at the feedlot during winter.

The current study showed that the overall development and survival rates of adult *C. hirtula* flies are better than those of *C. vagans*, except at 36°C, where the survival of *C. vagans* proved to be significantly better. However, at the feedlot *C. hirtula* accounted for less than 1% of the total number of Sphaeroceridae collected by using sweeping nets, in spite of laboratory studies proving their survival to be better than that of *C. vagans*. An explanation for this phenomenon would undoubtedly be complicated and a single factor such as temperature, although important, should not be looked at in isolation to explain it. A series of other factors are probably responsible for reducing the numbers of *C. hirtula* at the feedlot. Competition may also be important, and since *C. vagans* already established itself as the dominant population at Blokhuis feedlot, *C. hirtula* will most probably continue to occur in small numbers as a result of their direct competition with *C. vagans* for food and space. Other factors such as humidity and quality of dung might also play a role in determining survival of adult Sphaeroceridae, but these issues will be discussed in later chapters.

At Blokhuis feedlot near Harrismith, winter temperatures can sometimes be as low as -15°C. This indicates that both *C. vagans* and *C. hirtula* could probably not survive outdoors during winter without diapausing since they did not survive in the laboratory below 12°C. According to West (1951), other flies, for example house fly adults, survived at 0°C for a week and would then have hibernated in the adult stage. On the other hand, the temperature inside the dung is probably higher than the air temperature because of dung fermentation and heat generation. Temperature may therefore be elevated to levels where the immature stages of the Sphaeroceridae can survive during the cold winter months, although probably not in large numbers. Hammer (1941) mentioned that *C. lugubris*. in Denmark could continue their development through winter and remain active during the cold European winter months if conditions allow for active decomposition and an associated elevation of substrate temperature. Hafez (1941) mentioned that both *C. vagans* and *Coproica nigerrima* (Haliday) were present on dung during the winter months in Egypt when temperatures were below 10°C. Marshall (pers. comm.) stated that many Sphaeroceridae also remain active during Canadian winters without any diapause phase, provided the substrate temperature was high enough owing to fermentation processes. During some investigations at the feedlot in winter, a few Sphaeroceridae pupae were discovered in the dry dung underneath the fences of the camps, which could possibly mean that these flies hibernate in this stage. Among certain other Sphaeroceridae, another adaptive feature is an increased supercooling ability, which is of paramount importance, especially for species that live in harsh habitats like semi-polar and alpine regions or through cold winter seasons (Vernon & Vannier, 1996). An example of this special feature is found in the wingless sphaerocerid *A. aptera* which is an endemic fly from subantarctic islands of the South Indian Ocean, renowned for their geographic remoteness and cold, buffered oceanic climate (Vernon & Vannier, 1996).

To understand the effect of temperature on adult sphaerocerids more clearly, some physiological aspects might be relevant at this stage. Exactly what causes death to insects

at lower temperature limits is still in doubt (Lee & Denlinger, 1985b). A number of possibilities have been suggested, including disruption of the submicroscopic architecture of insect tissue by the formation of ice crystals at the lower end of the temperature range (Salt, 1961). At the upper limits, denaturation of proteins (Maynard-Smith, 1958) or even melting of cellular lipids and phosphatides (House *et al.*, 1958) may cause death. The possibility that a breakdown of homeostatic regulation is involved at the level of metabolic and physiological integration, is supported by Okasha (1968), who showed that exposure of some insects to sublethal temperatures caused a variety of complex physiological effects, including delayed moulting and inhibition of neuroendocrine activity.

In conducting temperature experiments, Lee & Denlinger (1985b) stated that valid comparisons between the tolerance to heat of different species could only be made when the duration of exposure was identical. Comparative studies of thermal resistance was further complicated by the phenomenon of acclimation and the fact that lethal temperatures may vary according to the thermal history of the population tested (Maynard-Smith, 1958). For example the LD_{50} for *Drosophila* sp. reared at a higher temperature is 154 ± 7 minutes, compared to a value of 105 ± 4 minutes for the control, while the LD_{50} increased to 220 ± 5 minutes for those flies that had been preconditioned for two hours at 36°C (Lee & Denlinger, 1985b). Therefore, for the purpose of comparing *C. vagans* and *C. hirtula*, it was imperative to keep both laboratory colonies under similar conditions.

3.3.7 Development at fluctuating environmental temperatures

3.3.7.1 Summer temperatures

The results obtained from these experiments, where the influence of fluctuating summer temperatures was tested on the development and survival of sphaerocerids, were

compared with 18°C and 24°C constant temperatures. The duration of the eggs stages of both *C. vagans* and *C. hirtula* were shorter at fluctuating summer temperatures than at 18°C or 24°C constant temperatures (Tables 3.1 & 3.2).

The development time of the larval stages of both species was longer at the fluctuating temperatures than at any of the two constant temperatures. However, the duration of the pupal stages at fluctuating summer temperatures was longer than at 24°C, but shorter compared to those at 18°C for both species (Tables 3.1 & 3.2). Survival of all immature stages of both species was generally higher at the fluctuating summer temperatures compared to those at the constant temperatures. Hatching of *C. vagans* eggs was much higher at fluctuating summer temperatures than at 18°C and 24°C constant temperatures.

Table 3.1: The average duration and mean percentage survival of the different development stages of *Coproica vagans* under fluctuating summer temperatures.

	18°C		Fluctuating temperatures		24°C	
	Duration (days)	% survival	Duration (days)	% survival	Duration (days)	% survival
Eggs	4.2	55.0	2.0	71.5	2.5	71.0
Larvae	7.0	37.0	8.0	88.5	4.2	67.0
Pupae	12.0	60.0	9.5	85.0	5.0	82.0
Adults	20.0	N/A	21.0	N/A	15.0	N/A

$\bar{x}$ Min. temperature: 11.1°C; $\bar{x}$ Max. temperature: 27.2°C; $\bar{x}$ Temperature: 20.2°C

Table 3.2: The average duration and mean percentage survival of the different development stages of *Coproica hirtula* under fluctuating summer temperatures.

	18°C		Fluctuating temperatures		24°C	
	Duration (days)	% survival	Duration (days)	% survival	Duration (days)	% survival
Eggs	4.5	25.0	2.0	74.5	2.4	36.0
Larvae	7.0	65.0	8.0	95.0	4.5	66.0
Pupae	12.5	78.0	9.0	90.0	4.5	88.0
Adults	25.0	N/A	19.0	N/A	18.0	N/A

$\bar{x}$ Min. temperature: 11.1°C; $\bar{x}$ Max. temperature: 27.2°C; $\bar{x}$ Temperature: 20.2°C

The survival of *C. hirtula* eggs at fluctuating temperatures was almost the same as those at 24°C, while at 18°C, hatching percentages were lower (Table 3.2). Survival of larvae and pupae of both species were also higher at fluctuating summer temperatures compared to those at constant temperatures of 18°C and 24°C (Tables 3.1 & 3.2). Adult flies of *C. vagans* and *C. hirtula* survived for 19 and 18 days respectively at these fluctuating summer temperatures, which was slightly shorter than adult life expectancy ranges at 18°C but also longer than adult life expectancies at 24°C constant temperatures (Tables 3.1 & 3.2).

3.3.7.2 Winter temperatures

The mean fluctuating temperature during the winter in Bloemfontein was 7.3°C and the survival of *C. vagans* and *C. hirtula* was compared to the results which were obtained at a constant temperature of 6°C in the laboratory. The survival of the different development stages of both species at fluctuating winter temperatures was higher than those at lower constant temperatures. At fluctuating winter temperatures (Table 3.3), egg

survival was 2% and 1.5% for *C. vagans* and *C. hirtula* respectively, in comparison to the 0% egg survival at 6°C constant temperature. The duration of the egg stages for both species was 15.3 ± 1.2 days for *C. vagans* and 16.7 ± 1.3 days for *C. hirtula* (Table 3.3).

The survival of larvae and pupae of both *C. vagans* and *C. hirtula* was higher at fluctuating winter temperatures, especially the pupal survival, compared to the survival at 6°C constant temperature where presumably no larvae or pupae could have survived. The larval stages showed survival of 14.5% and 17% for *C. vagans* and *C. hirtula* respectively (Table 3.3), while the pupal survival of *C. vagans* and *C. hirtula* was 58.5% and 70.8% respectively at fluctuating winter temperatures (Table 3.3).

Table 3.3: The average duration and mean percentage survival of the different development stages of both *Coproica vagans* and *Coproica hirtula* under fluctuating winter temperatures.

	C. vagans		*C. hirtula*	
Winter conditions	Duration	%	Duration	%
Eggs	15.3	2.00	16.7	1.50
Larvae	14.3	14.5	14.4	17.0
Pupae	23.5	58.4	23.8	70.8
Adult flies	-	-	-	-

$\bar{x}$ Min. temperature: -4.5°C; $\bar{x}$ Max. temperature: 15.6°C; $\bar{x}$ Temperature: 7.3°C

Results indicated that fluctuating summer temperatures tend to slow the development of larvae, although an increase in the percentage larval survival of the Sphaeroceridae was significant. In Britain, Laurence (1954) also found that most species of Diptera living as larvae in cow pats during summer have development periods of less than 40 days. It therefore seems as if fluctuating temperatures, irrespective whether in summer or in winter caused the development rates of the immature stages of the sphaerocerids to be

faster compared to constant temperatures. Although the mean temperature during the summer was 20.2°C, the temperatures fluctuated from 11°C at night to 27°C at midday, and this phenomenon undoubtedly contributed to the velocity of immature development of Sphaeroceridae. Laurence (1954) found that in winter the sphaerocerid larvae in a pat in Britain develop much more rapidly if the temperature is raised with a few degrees. Messenger (1964) also stated that temperature exerted a dominant effect on the growth of bushfly larvae in Australia, and was able to show that fluctuating temperatures increased development rates, compared with a steady temperature equaling the means of the fluctuations.

The phenomenon of acclimation, whether developmental or physiological, is likely to be of considerable significance to Sphaeroceridae living at feedlots. Recently it has been documented that insects reared at specific temperatures display different tolerances and behaviour when exposed to subsequent hot (Hallman, 1994) and cold (Iwata *et al.*, 1992) environments. Lee & Denlinger (1985b) maintained that the season during which there is the greatest danger of exposure to lethal high temperatures will be preceded by months during which the mean temperatures are gradually rising, so that the process of development acclimation may be in some measure fit for the flies to withstand high temperatures. Moreover, the time of day during which critical temperatures are likely to be approached, will be preceded by hours during which the flies will be exposed to high sublethal temperatures, thus enabling a certain amount of physiological acclimation to take place (Lee & Denlinger, 1985b). The cumulative effect of these processes may well raise the mortality threshold by a degree or more, which must be taken into account in applying laboratory data to field conditions. It is known that laboratory-reared flies were used in this study and that some aspects of the ecology of laboratory flies may differ from their wild counterparts, although it is important to emphasize that all the flies used in this study have the same origin. According to Karandinos & Axtell (1967) fluctuations in the soil and dung temperatures are often minor compared to fluctuations in air temperature. They therefore concluded that it might be possible to use data obtained from

from constant temperature experiments and climatological data to make approximate predictions of the emergence flies in the field.

In general, Hammer (1941) found that the various cattle dung flies have a very rapid development because the medium in which they live is suitable only for a short period. According to Hammer (1941) there appears to be a tendency among the coprophagous muscids to develop more rapidly than parasitic or predatory muscids. On the other hand, flies that have a long development time, *e.g.* Stratiomyiidae, show greater resistance to desiccation (Hammer, 1941). The concept of K- and r- selection is of some relevance here. To maximize reproductive rates in harsh, unstable environments where populations remain well below the carrying capacity of the environment and resources are not limiting except for the period necessary to reproduce successfully, a r-selective strategy will be followed (Price, 1984). At the other end of the continuum, in predictable, stable environments populations will frequently reach the carrying capacity of the environment and selection will operate towards improving adaptive traits for living in these crowded, competitive conditions, where enemies such as predators and parasites are present, and these will be very effective K-selectors (MacArthur & Wilson, 1967).

In retrospect, this study gave good insight into the life cycle of both sphaerocerid species in question. It became clear that temperature had a major effect on development and survival of all development stages in the complete life cycle of Sphaeroceridae. The results also showed that fluctuating summer temperatures caused a significant increase in survival of *Coproica* species, and at fluctuating winter temperatures, survival of immature stages were also better compared to lower constant temperatures. It could also be that these studies which were conducted at constant temperatures can somewhat obscure the perceptions on what effect temperature had on the life cycle of the flies. Rearing at constant temperatures could therefore have severe drawbacks because constant temperatures did not have the same effect as fluctuating temperatures.

3.4 APPENDIX

Table A3.1: Analysis of variance of the development time for the eggs of *Coproica vagans* at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	1435.48	4	358.87	35.07143	2.85E-46	2.578737
Error	11.9	45	0.264444			
Total	1447.38	49				

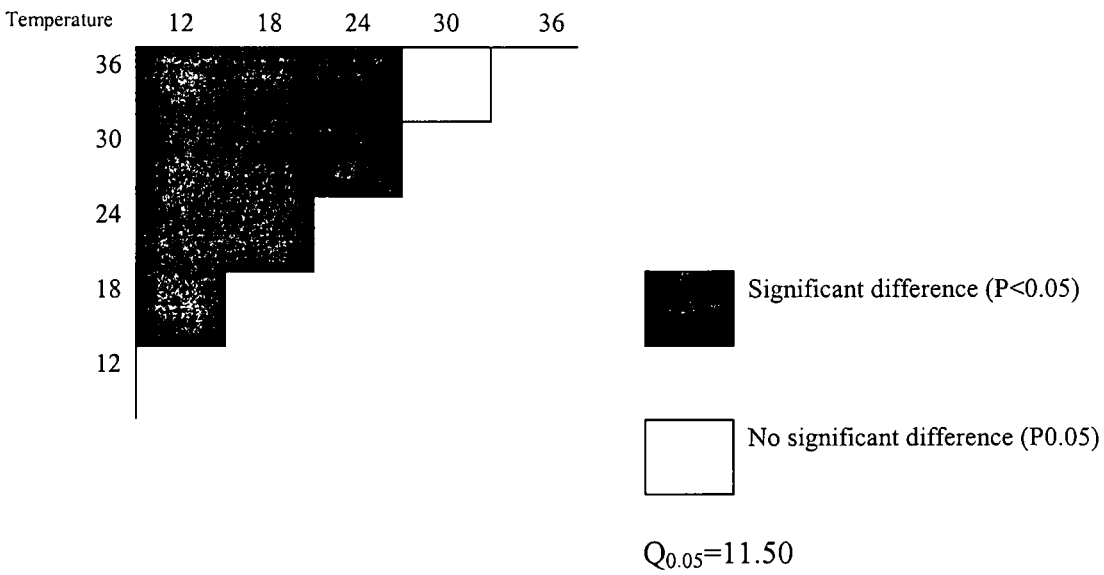


Figure A3.1: A schematic presentation of the significant differences in development time of *Coproica vagans* eggs at different constant temperatures.

Table A3.2: Analysis of variance of the development time for the eggs of *Coproica hirtula* at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	1393.12	4	348.28	49.62857	3.4E-47	2.578737
Error	10.5	45	0.233333			
Total	1403.62	49				

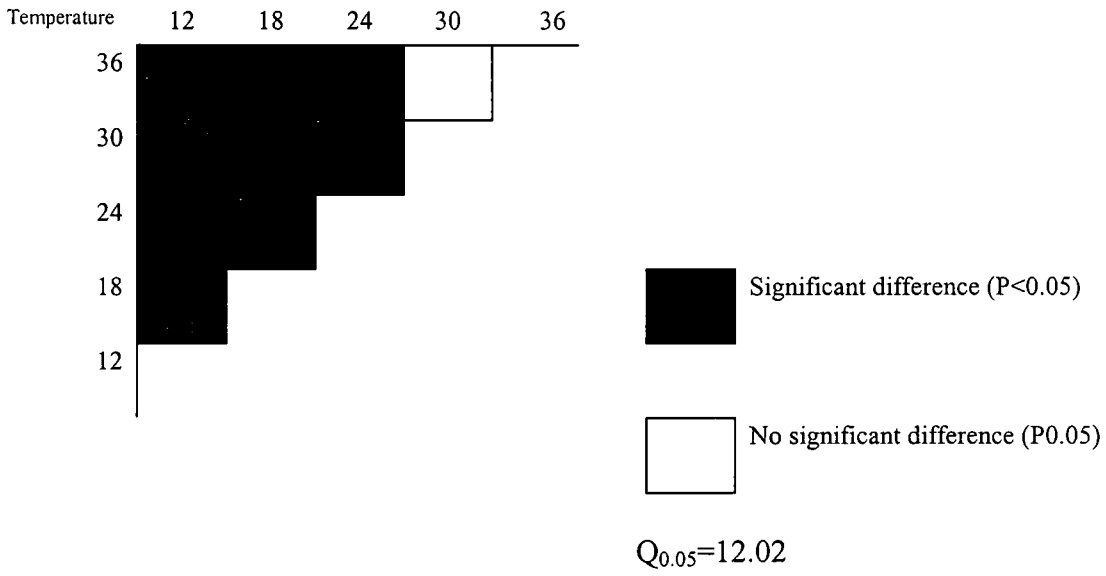


Figure A3.2: A schematic presentation of the significant differences in development time of *Coproica hirtula* eggs at different constant temperatures.

Table A3.3: Analysis of variance of the percentage hatching of the eggs of *Coproica vagans* at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	24726.88	4	6181.72	41.03154	1.82E-14	2.578737
Error	6779.6	45	150.6578			
Total	31506.48	49				

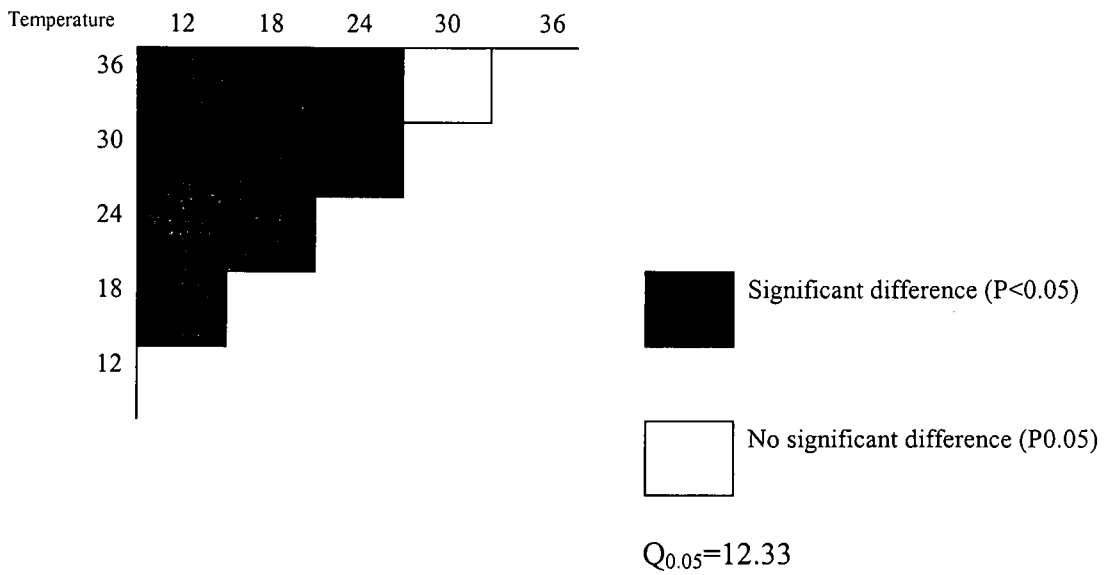


Figure A3.3: A schematic presentation of the significant differences in hatching of *Coproica vagans* eggs at different constant temperatures.

Table A3.4: Analysis of variance of the percentage hatching of the eggs of *Coproica hirtula* at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	9863	4	2465.75	14.87881	8.05E-08	2.578737
Error	7457.5	45	165.7222			
Total	17320.5	49				

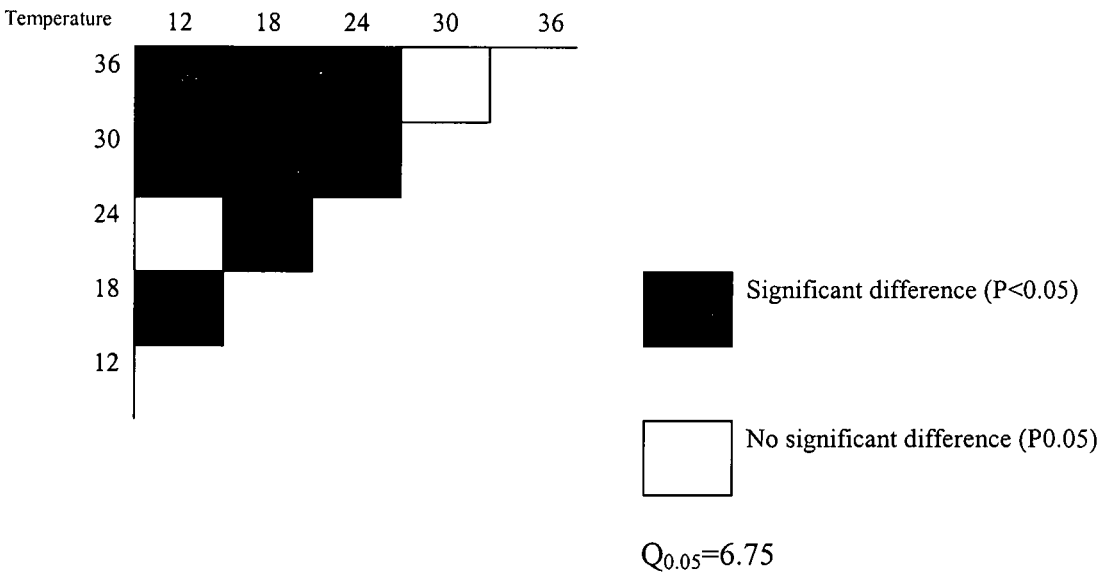


Figure A3.4: A schematic presentation of the significant differences in hatching of *Coproica hirtula* eggs at different constant temperatures.

Table A3.5: Analysis of variance of the development time for the larvae of *Coproica vagans* at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	4293.68	4	1073.42	56.85112	2.86E-46	2.578737
Error	35.6	70	0.791111			
Total	4329.28	74				

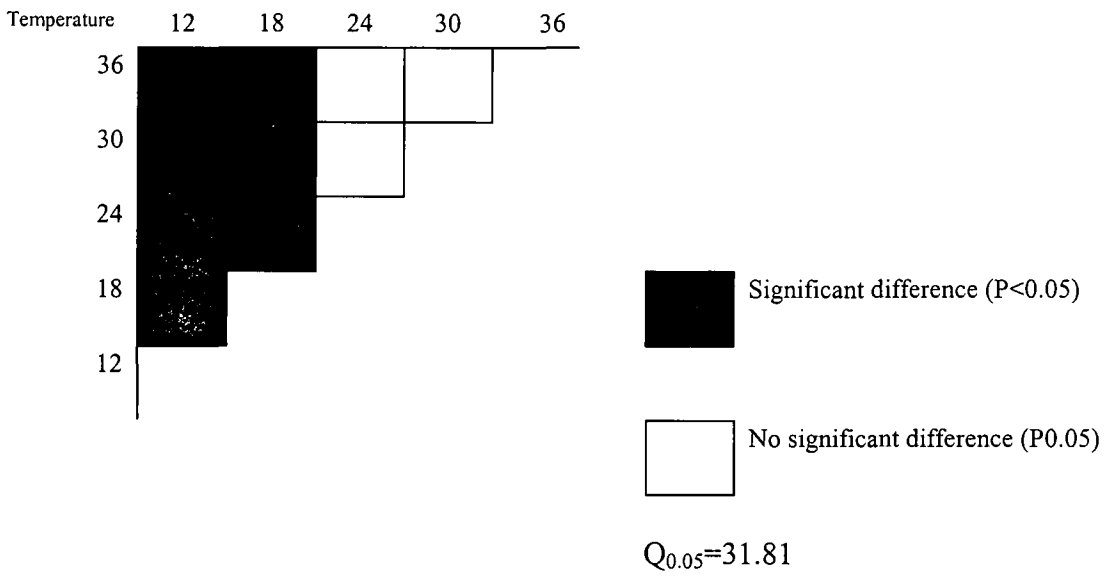


Figure A3.5: A schematic presentation of the significant differences in development time of *Coproica vagans* larvae at different constant temperatures.

Table A3.6: Analysis of variance of the development time for the larvae of *Coproica hirtula* at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	4320.28	4	1080.07	80.11667	5.18E-49	2.578737
Error	27	70	0.6			
Total	4347.28	74				

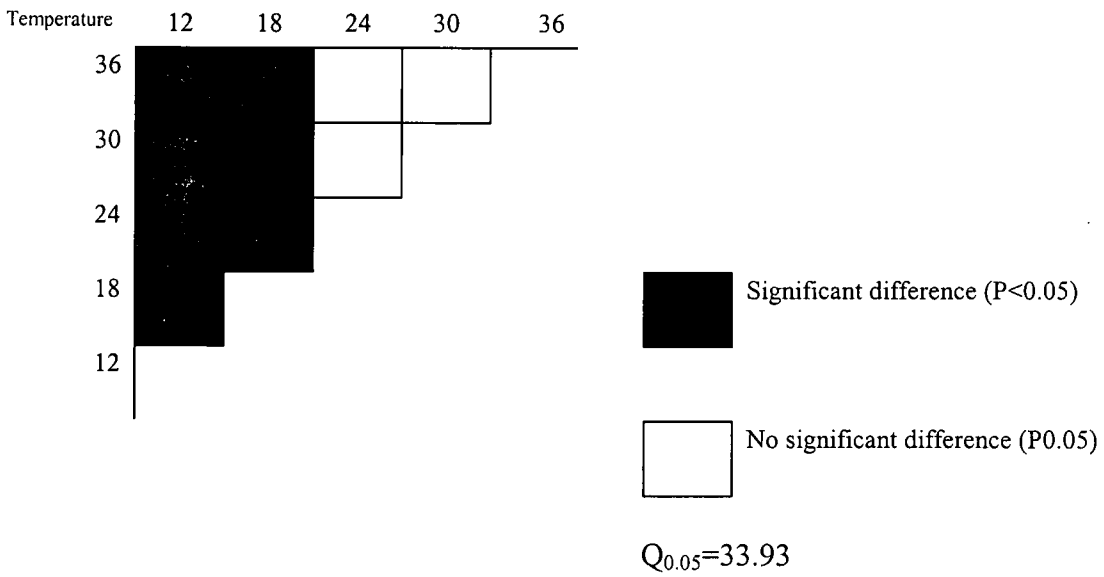


Figure A3.6: A schematic presentation of the significant differences in development time of *Coproica hirtula* larvae at different constant temperatures.

Table A3.7: Analysis of variance of the percentage survival of larvae of *Coproica vagans* at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	18933	4	4733.25	26.24723	2.88E-11	2.578737
Error	8115	70	180.3333			
Total	27048	74				

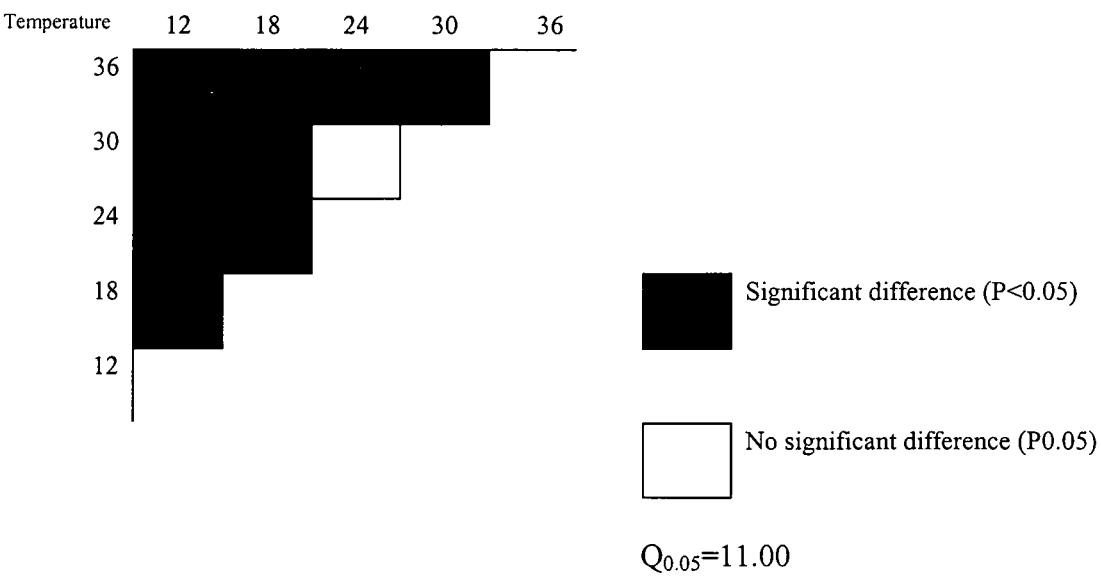


Figure A3.7: A schematic presentation of the significant differences in survival of *Coproica vagans* larvae at different constant temperatures.

Table A3.8: Analysis of variance of the percentage survival of larvae of *Coproica hirtula* at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	437	4	109.25	0.485076	0.746564	2.578737
Error	10135	70	225.2222			
Total	10572	74				

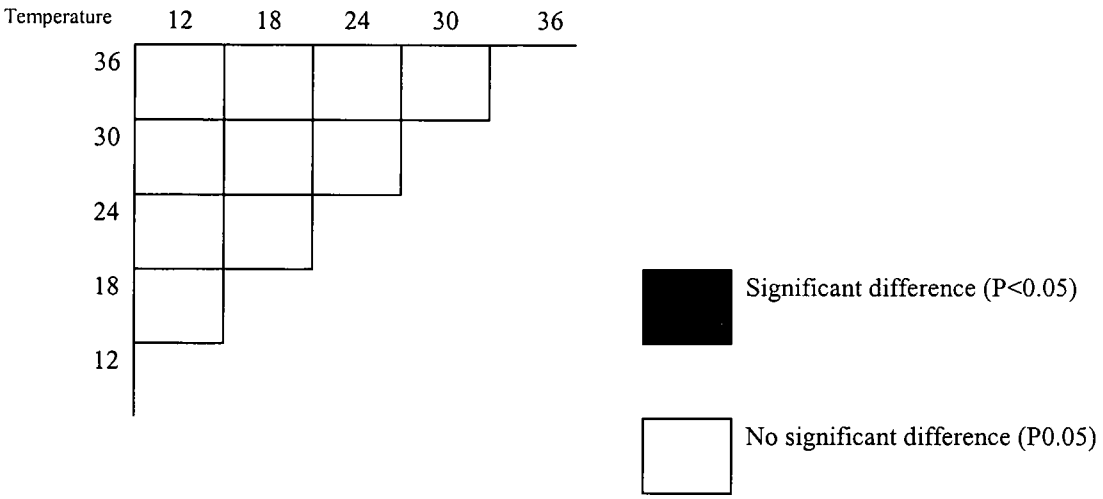


Figure A3.8: A schematic presentation of the significant differences in survival of *Coproica hirtula* larvae at different constant temperatures.

Table A3.9: Analysis of variance of the development time for the pupae of *Coproica vagans* at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	8462.52	4	2115.63	38.01047	2.17E-40	2.578737
Error	129	55	2.866667			
Total	8591.52	59				

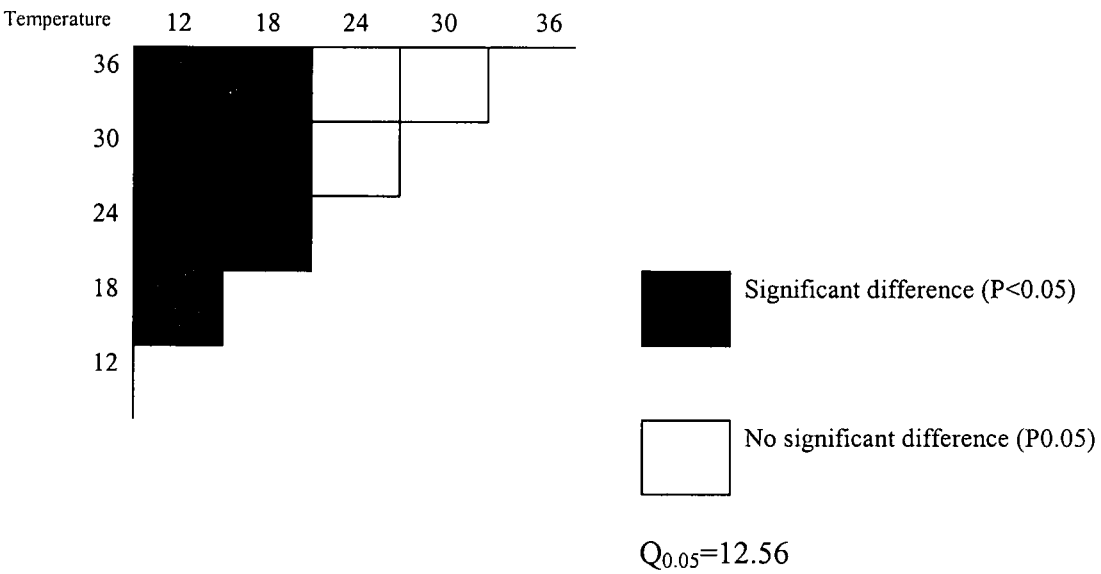


Figure A3.9: A schematic presentation of the significant differences in development time of *Coproica vagans* pupae at different constant temperatures.

Table A3.10: Analysis of variance of the development time for the pupae of *Coproica hirtula* at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	8258.68	4	2064.67	87.94087	3.92E-44	2.578737
Error	85.4	55	1.897778			
Total	8344.08	59				

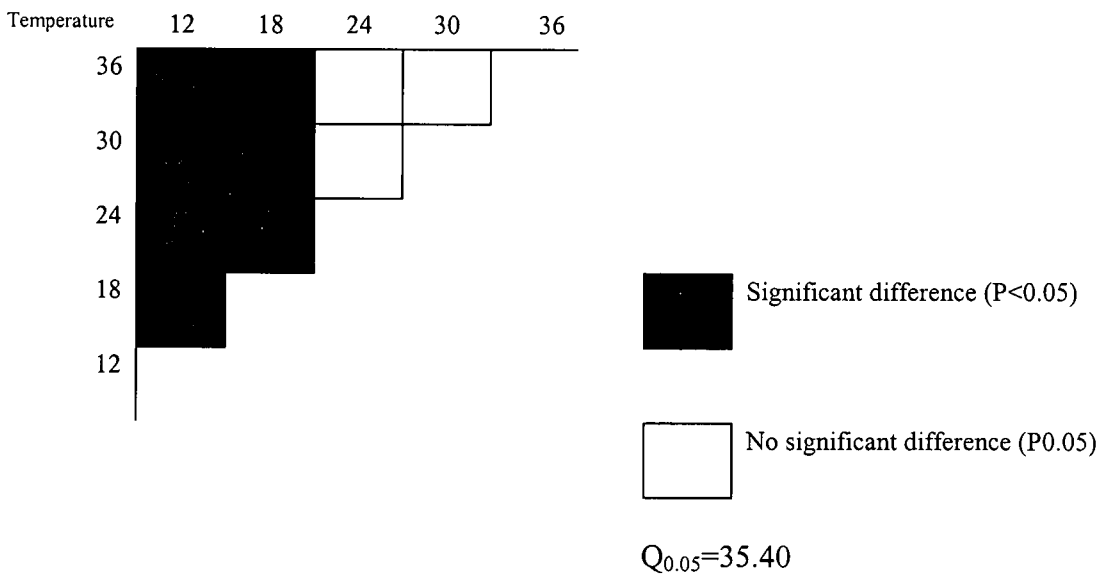


Figure A3.10: A schematic presentation of the significant differences in development time of *Coproica hirtula* pupae at different constant temperatures.

Table A3.11: Analysis of variance of the percentage survival of pupae of *Coproica vagans* at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	31476.2	4	7869.05	26.25779	2.87E-11	2.578737
Error	13485.8	55	299.6844			
Total	44962	59				

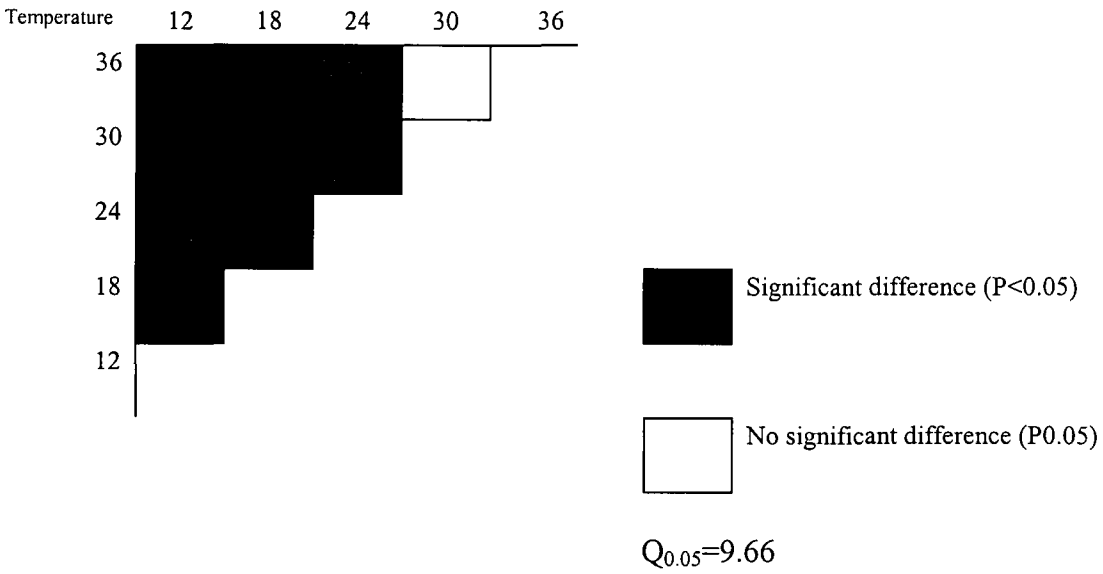


Figure A3.11: A schematic presentation of the significant differences in survival of *Coproica vagans* pupae at different constant temperatures.

Table A3.12: Analysis of variance of the percentage survival of pupae of *Coproica hirtula* at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	39282	4	9820.5	37.25918	1.44E-19	2.578737
Error	5720	55	127.1111			
Total	45002	59				

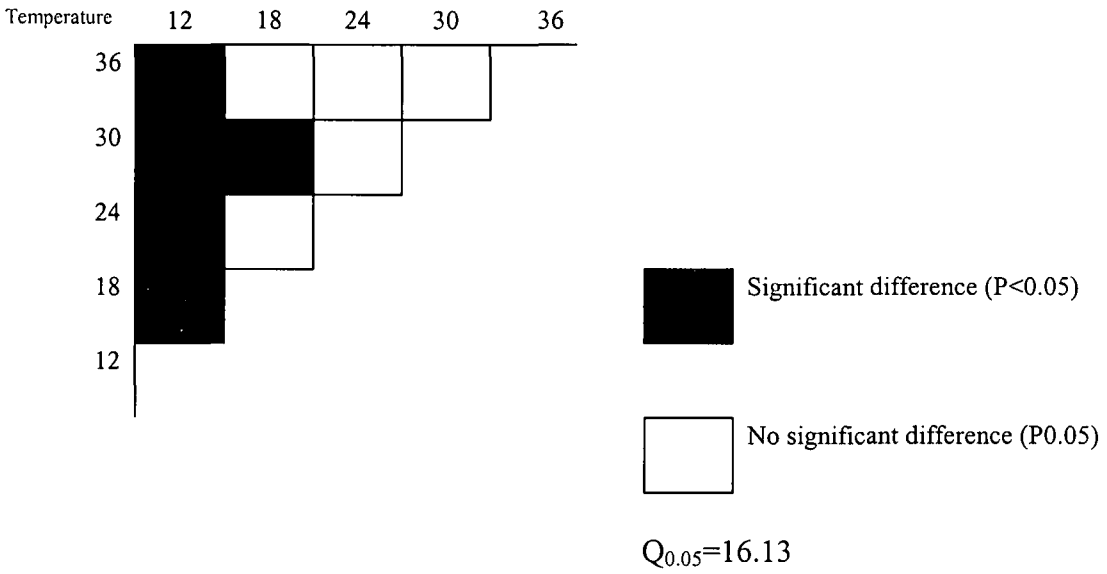


Figure A3.12: A schematic presentation of the significant differences in survival of *Coproica hirtula* pupae at different constant temperatures.

Table A3.13: Analysis of variance of the percentage emergence of adult flies of *Coproica vagans* at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	6172.4988	4	1543.125	14.62301	9.98E-08	2.578737
Error	4748.723	70	105.5272			
Total	10921.222	74				

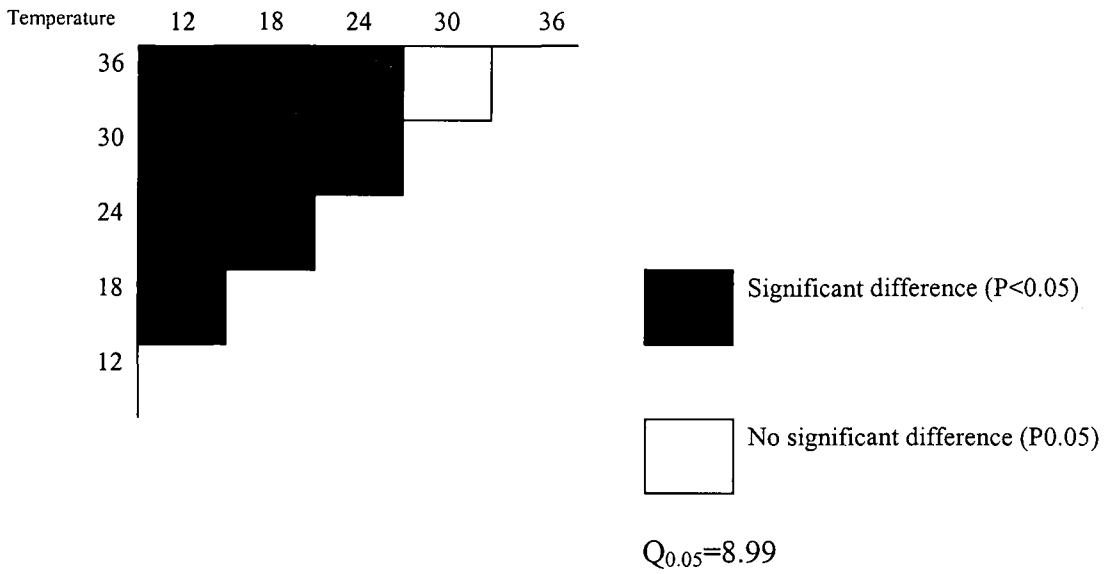


Figure A3.13: A schematic presentation of the significant differences in the percentage *Coproica vagans* eggs that developed to adulthood at different constant temperatures.

Table A3.14: Analysis of variance of the percentage emergence of adult flies of *Coproica hirtula* at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	5129.48	4	1282.37	34.68066	3.12E-33	2.578737
Error	165.5	70	3.677778			
Total	5294.98	74				

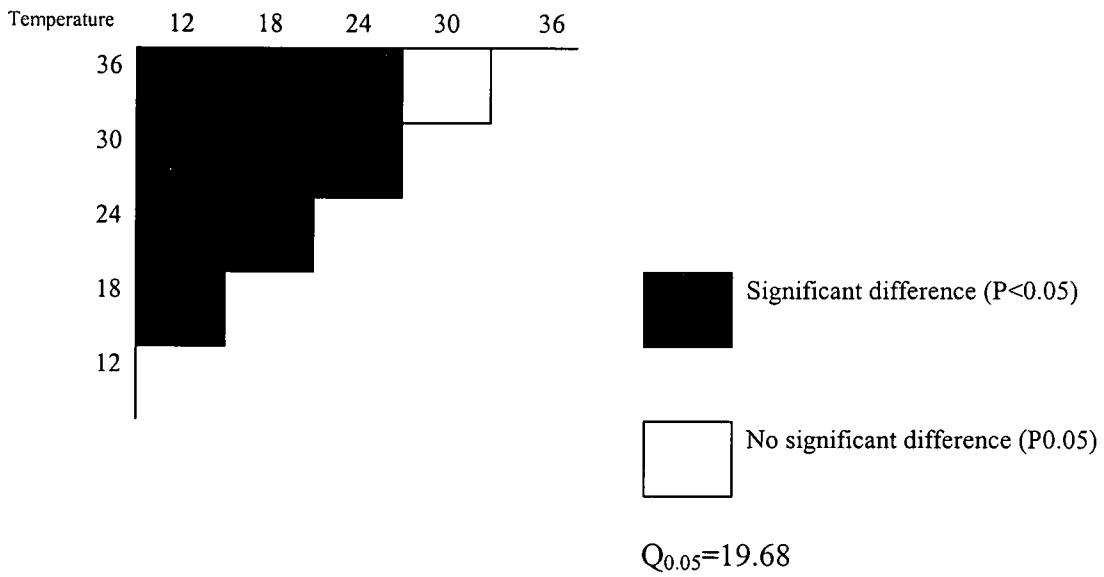


Figure A3.14: A schematic presentation of the significant differences in the percentage *Coproica hirtula* eggs that developed to adulthood at different constant temperatures.

Table A3.15: Analysis of variance of the life expectancy of adult flies of *Coproica vagans* at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	6464.6	4	1616.15	25.54146	4.39E-11	2.578737
Error	2847.4	45	63.27556			
Total	9312	49				

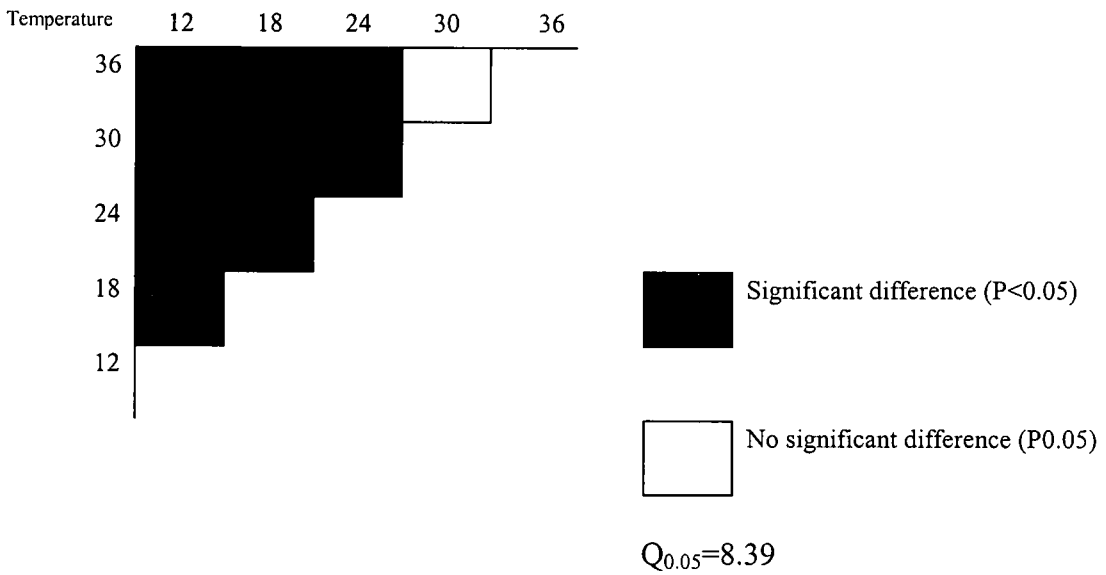


Figure A3.15: A schematic presentation of the significant differences in life expectancy of *Coproica vagans* adults at different constant temperatures.

Table A3.16: Analysis of variance of the life expectancy of adult flies of *Coproica hirtula* at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	8938.88	4	2234.72	34.175	3.02E-33	2.578737
Error	288	45	6.4			
Total	9226.88	49				

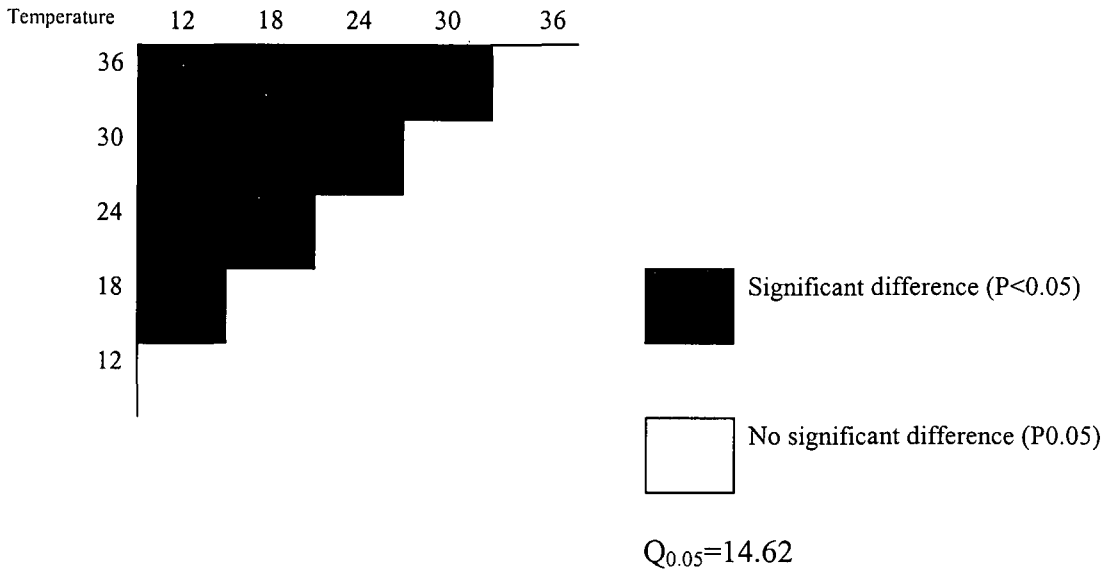


Figure A3.16: A schematic presentation of the significant differences in life expectancy of *Coproica hirtula* adults at different constant temperatures.

Table A 3.17: Results from t-tests (indicated by P-values) in comparing development times between *Coproica vagans* and *Coproica hirtula* of all stages at different constant temperatures.

Temperature(°C)	12	18	24	30	36
Eggs	0.641	0.785	0.841	0.744	0.997
Larvae	0.891	0.956	0.787	0.989	0.990
Pupae	0.479*	0.799	0.953	0.815	0.992

(* indicate significant difference [P<0.05])

Table A 3.18: Results from t-tests (indicated by P-values) in comparing survival rates between *Coproica vagans* and *Coproica hirtula* of all stages at different constant temperatures.

Temperature(°C)	12	18	24	30	36
Eggs	0.002*	0.002*	0.003*	0.039*	0.044*
Larvae	0.001*	0.005*	0.879	0.043*	0.032*
Pupae	0.033*	0.029*	0.766	0.035*	0.037*

(* indicate significant difference [P<0.05])

Table A 3.19: Results from t-tests (indicated by P-values) in comparing adult survival and life expectancy between *Coproica vagans* and *Coproica hirtula* of all stages at different constant temperatures.

Temperature(°C)	12	18	24	30	36
% Eggs developing to adulthood	0.040*	0.676	0.002*	0.029*	0.033*
Life-expectancy	0.042*	0.035*	0.048*	0.317	0.039*

(* indicate significant difference [P<0.05])

CHAPTER 4

THE INFLUENCE OF DIFFERENT MOISTURE CONTENTS ON THE LIFE CYCLES OF *COPROICA VAGANS* AND *COPROICA HIRTULA*

4.1 INTRODUCTION

The influence of moisture on the development and survival of Diptera has attracted the attention of many scientists. Mohr (1943) found that dry weather prevents development of horn fly, *H. irritans*, in the USA, whereas a series of showers invariably brought about a sudden and conspicuous increase in numbers. However, both too much and too little rain may cause a decline in numbers (Bruce, 1939). Hammer (1941) indicated that low water content of the manure could become a limiting factor in the development of face fly larvae in Denmark if the dung became too dry to allow feeding. Although most dung inhabitants have a short life cycle due to rapid physical changes in the dung (Hammer, 1941), certain species are able to tolerate dry conditions in the dung for long periods (Hammer 1941). Mohr (1943) found that dung is frequently so wet that when dropped, it spreads thinly. The horn fly often perishes in these thin, watery faeces especially during warm weather, due to rapid moisture evaporation and subsequent desiccation. The genus *Sarcophaga* (Sarcophagidae) seems to avoid such thin watery droppings, while other groups usually oviposit large numbers of eggs, but are subsequently prevented from completing development because the dung dries out too quickly (Mohr, 1943). Fredeen & Taylor (1964) described the infestation of modern septic sewage disposal tanks by *L. caenosa.* They demonstrated that this species is also adapted to particularly high humidity conditions.

The above-mentioned information and the apparent lack of knowledge of the moisture preferences of the Sphaeroceridae prompted an investigation into the following questions:

(1): What influence would different moisture content have on the development and survival of *C. vagans* and *C. hirtula*? This information is needed to improve the forecasting model for Sphaeroceridae control at feedlots.

(2): What would the optimum moisture conditions be for successfully maintaining healthy laboratory colonies?

(3): Should the wet areas at the feedlot be treated with insecticides to control Sphaeroceridae?

4.2 MATERIAL AND METHODS

To create rearing media with different moisture content, a fixed amount of distilled water was added to a known amount of dried dung (Table 4.1). Cattle dung was dried for two weeks in an oven at 120°C and ground to a fine powder. The moisture content of the re-hydrated dung ranged from 40% to 100% with 10% intervals. The moisture range started at 40% moisture content because preliminary results indicated that neither egg nor larval development nor any adult survival occurred at 30% moisture content. This implied that no development was possible at 30% moisture content, although pupal survival and development occurred.

For this experiment it was essential to maintain constant moisture content in the dung. The effects of evaporation were therefore determined beforehand by monitoring the mass loss over a 24-hour period in dung with a 100% moisture content (see Table 4.2). The results showed that the average mass difference over a 24-hour period was 3.8% (Table 4.2).

Table 4.1: The different dung/water ratios used to create rearing media of different moisture content.

MOISTURE CONTENT (%)	DUNG/WATER RATIO*
40	0.40 : 1
50	0.50 : 1
60	0.60 : 1
70	0.70 : 1
80	0.80 : 1
90	0.90: 1
100	1.00 : 1

*Dung/Water Ratio : 0.4 - 1.0 kg of dung + 1litre water.

Table 4.2: Mass difference owing to evaporation from the 100% moisture content vials at 24°C monitored over a 24-hour period.

Replicates	Mass difference	Percentage difference
1	0.07	3.8
2	0.07	4.3
3	0.09	5.3
4	0.04	2.1
5	0.08	4.8
6	0.10	5.9
7	0.10	5.9
8	0.07	4.1
9	0.03	5.1
10	0.03	1.8

$\bar{x}$=3.8 %

The development and survival experiments were conducted in glass vials (Apex No. 8 - 75 x 25 mm) at a temperature of 24°C. At the onset of each experiment, dung of different moisture content (40% - 100%) was placed in the vials to a depth of one centimetre. Each vial was weighed every 12 hours. The distilled water was kept at 24°C to avoid a temperature change in the rearing medium with the addition of water. The prepared vials were preconditioned by exposing them to 24°C (the optimum temperature) (see 3.3.2) for 24 hours before the onset of the experiments.

4.2.1 Egg development

Individual females from laboratory colonies (F2) of *C. vagans* and *C. hirtula* were introduced separately to the prepared vials and allowed to oviposit on dung of different moisture contents. After 24 hours the females were removed and the number of eggs oviposited were counted and allowed to hatch. Unfortunately the distribution of eggs was rather uneven, especially on dry dung (40% moisture content) where very few eggs were oviposited. Therefore a number of eggs had to be transferred to these vials from adjacent 50 % and 60% moisture content vials before the eggs were counted. The development period of the eggs at each of the moisture contents was recorded and the percentage hatching calculated from the number of eggs oviposited in each of the vials.

4.2.2 Larval development

Larvae that hatched from the egg development experiment (see 4.2.1) were used to determine larval development. Fifty first instar larvae (approximately 12 hours old) of *C. vagans* and *C. hirtula* were introduced separately to individual Apex vials containing rearing medium of different moisture contents. Larval development times and survival were monitored from first instar to pupation. No distinction was made between the different instars. At the end of the larval stage, the number of pupae that formed was counted and documented. Vials were closed with perforated stoppers to facilitate

ventilation. The experiment was conducted in a temperature-controlled incubator set at 24 ± 1°C with a day-night cycle of 12 hours light and 12 hours dark. Relative humidities in the incubators were monitored with hygrometers throughout the experiment. Moisture loss was detected and rectified by weighing individual vials daily. The number of surviving individuals was counted every 12 hours. There were 10 replicates in each treatment and the experiment was repeated three times, for each of the two species. The same experimental procedure was followed to determine larval, pupal, adult and total development and survival at different moisture content for *C. vagans* and *C. hirtula*.

4.2.3 Pupal development

Pupal development time and survival were determined by introducing 50 pupae (approximately 12 hours old) of *C. vagans* and *C. hirtula* separately to different Apex vials (No. 8) containing rearing medium of different moisture content. The pupae originated mainly from the larvae reared in the larval development experiment. It was found that at the 40% moisture content, very few larvae survived, and pupae were substituted from the laboratory colonies (see 3.2.1). These pupae were carefully selected to ensure that those taken from the larval development experiment and those taken from the laboratory colonies were not older than 12 hours. This was determined by observing the movements of larvae. Just prior to pupation their movements slowed down and within a few hours the larvae pupated. These pupae were collected and used in the experiments. The development times and survival of pupae were recorded for both *C. vagans* and *C. hirtula*.

4.2.4 Total immature development

Individual *C. vagans* and *C. hirtula* females from the laboratory colonies were kept in Apex vials (no.8) for one day and allowed to oviposit as described in the egg development experiment (see 4.2.1). The number of eggs was determined and allowed to

hatch. The larvae were left undisturbed in the original vials for the duration of the immature development (See Table 4.1). The total immature development time and percentage survival (from oviposition to pupal emergence) were determined from the number of eggs oviposited by both *C. vagans* and *C. hirtula*.

4.2.5 Adult survival

To determine adult survival, 24-hour-old unsexed *C. vagans* and *C. hirtula* flies (F2) were randomly selected from the laboratory colonies The flies were kept individually in glass vials (Apex No. 8) containing a one centimetre layer of dung with moisture contents ranging from 40% to 100%. The vials were covered with perforated stoppers to facilitate ventilation and to prevent the flies from escaping. The number of surviving flies was determined every 12 hours until all the flies had died. The 12-hour period from introduction to the onset of the experiment was included in the calculations.

4.3 RESULTS AND DISCUSSION

4.3.1 Development of eggs

For both *C. vagans* and *C. hirtula* an increase in the moisture content led to a change in development time (Fig. 4.1). For *C. vagans*, the development time at 100 % moisture content was only 2.3 ± 0.1 days, while for *C. hirtula* it was 2.5 ± 0.2 days. At the lower moisture content (40%), the development times for *C. vagans* and *C. hirtula* were 6.0 ± 0.4 days and 5.5 ± 0.45 days respectively (Fig. 4.1). The development time of the egg stages of both species was plotted against moisture content, and a good statistical exponential relationship was shown to exist for both *C. vagans* ($r = 0.99$) and *C. hirtula* ($r = 0.98$) (Fig. 4.1). No development time data were obtained for moisture contents below 40% because no eggs survived below this level. As a result, threshold calculations could not be made for the eggs or any of the other immature stages of Sphaeroceridae.

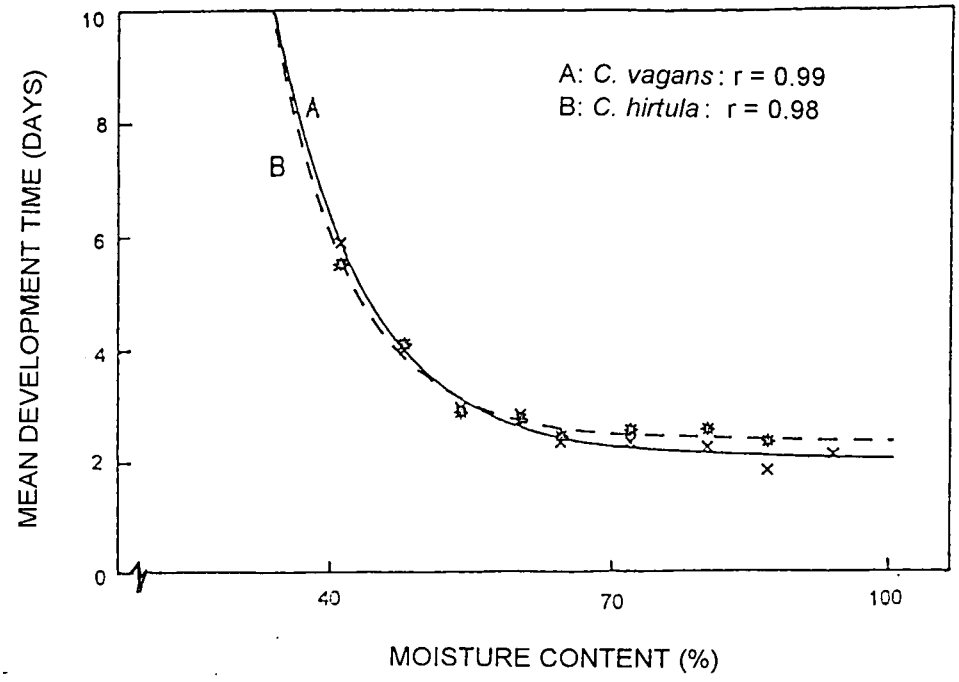


Figure 4.1: The exponential relationship of the mean development time for the egg stage of *Coproica vagans* and *Coproica hirtula* on dung of different moisture content.

With analysis of variance ($F_{63;6}$=64.63) it was shown that, for *C. vagans*, significant differences ($P<0.05$) occurred in egg development time (Table A4.1). Tukey's test ($Q_{0.05}$=15.30) showed that egg development times at moisture content of 40% and 50% differed significantly from each other. At 40% and 50% moisture content, eggs also took significantly longer to develop than at all the other treatments (Fig. A4.1). The same applied to *C. hirtula*, and with analysis of variance ($F_{63;6}$=51.72), significant differences ($P<0.05$) in the egg development times were shown between the different moisture treatments (Table A4.2). Tukey's test ($Q_{0.05}$=18.66) indicated that egg development times at 40% and 50% moisture content differed significantly from each other and also from all other higher moisture contents, as was the case in *C. vagans* (Fig. A4.2). From Fig. 4.1 it can also be seen that at lower moisture content (except at 50%), *C. vagans* eggs took significantly longer to develop compared to *C. hirtula* eggs, while at higher moisture content (80% - 100%), *C. hirtula* egg development was longer. To compare the

egg development times of *C. vagans* and *C. hirtula* statistically with each other, a t-test was applied to the data to compare the means obtained for the two species. Although there was not much difference between the two species at the higher moisture contents, these small differences were still significant ($P<0.05$) at all the moisture contents that were tested (Table A4.17).

Hatching of *C. vagans* and *C. hirtula* eggs occurred in dung with moisture contents ranging from 40% to 100% (Fig. 4.2). The highest hatching percentages were 72 ± 5.8% for *C. vagans* and 70 ± 6.0% for *C. hirtula* both at a moisture content of 90% (Fig. 4.2). Hatching percentages steadily decreased below and above 90% (Fig. 4.2). The lowest hatching percentage of 1.0 ± 0.05% for *C. vagans* and 11.0 ± 1.2% for *C. hirtula* occurred at 40% moisture content (Fig. 4.2). At moisture content of 80% and lower, the hatching percentage dropped to below 50% (Fig. 4.2). At 100% moisture content, the hatching percentages of *C. vagans* and *C. hirtula* eggs were 58 ± 4.8% and 55 ± 4.5% respectively.

Analysis of variance ($F_{63;6}=80.93$) showed that significant differences ($P<0.05$) occurred in the hatching percentage between the treatments of different moisture contents for *C. vagans* (Table A4.3). With Tukey's test ($Q_{0.05}=34.72$) it was shown that significant differences occurred between the hatching percentages at 90% and the rest of the moisture contents that were tested (Fig. A4.3). The hatching percentage at 40% was also significantly lower than the rest of the moisture treatments. Hatching percentages at the other moisture contents also differed significantly from one another, as indicated in Fig A4.3. For *C. hirtula*, analysis of variance ($F_{63;6}=21.78$) also showed significant differences ($P<0.05$) in egg hatching percentages (Table A4.4), while Tukey's test ($Q_{0.05}=15.98$) indicated that hatching percentages at 90% moisture content were significantly higher than those at other treatments (Fig. A4.4). Significant differences in the hatching of *C. hirtula* eggs were shown between all moisture contents. The only exception was between 70% and 80% moisture content (Fig. A4.4). Significant

differences ($P<0.05$) were also shown between the survival rates of *C. vagans* and *C. hirtula* eggs at all the moisture treatments (Table A4.18). These statistical differences were determined by using a t-test that was designed to compare the mean of two samples.

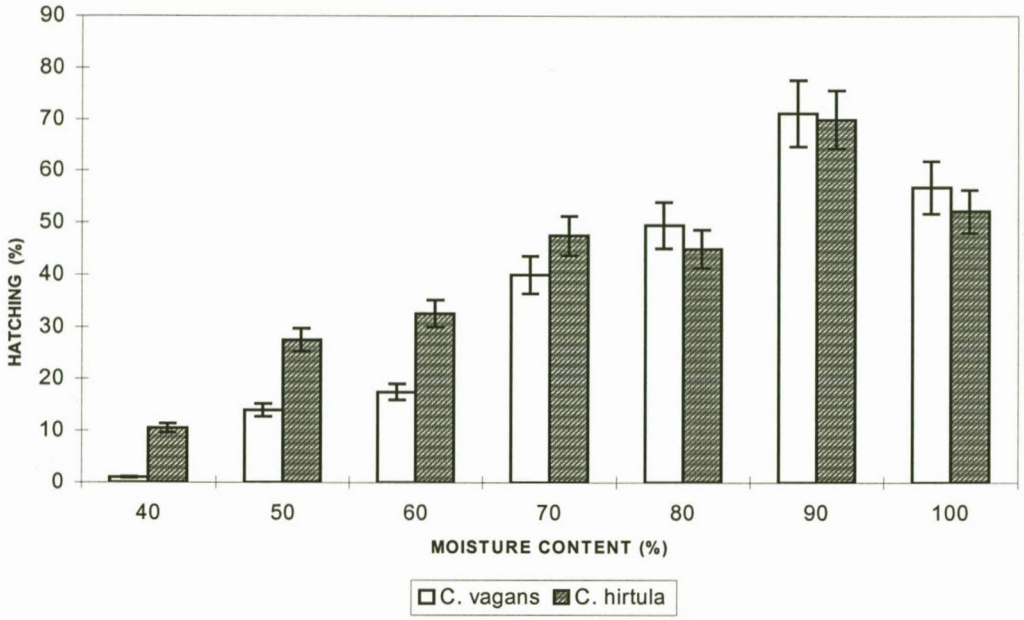


Figure 4.2: The hatching percentage of eggs of *Coproica vagans* and *Coproica hirtula* after exposure to dung of different moisture content.

From the results it became clear that the egg is an extremely vulnerable stage in the life cycle of these two Sphaeroceridae species because both too low or high moisture content negatively influenced the eggs. Humidity affected the rate of development of the egg stage in both sphaerocerid species in such a way that development times increased as the moisture content of the dung decreased below 80%. An insignificant increase in egg development time of *C. hirtula* was also observed above 80% moisture content. These results correspond with examples from the literature involving embryonic development, that were quoted in a review by Buxton (1936), who noted that development is usually retarded by low humidities. It has also been confirmed by Evans (1934) that *Lucilia*

sericata Meigen in Britain, maintained at 20°C, showed a decrease in incubation time for the eggs as humidities increased. Similar results were also obtained with *M. domestica* in Denmark (Larsen, 1943). Brust & Costello (1969) noted that the eggs of *Aedes vexans* (Meigen) in Manitoba, Canada showed a delay in hatching that appeared to be directly related to the amount of desiccation, indicating the necessity for the eggs to take up some moisture before hatching can occur. This is also the view of Valiela (1974) who found that in the case of the face flies, *M. autumnalis* in the state of New York, USA, the highest mortality occurred during the egg stage, especially at low humidities. However, Hammer (1941) indicated that this should only be a consideration on hot and sunny days, because on cloudy and rainy days the desiccation of eggs is minimized. Hammer (1941) maintained that rainy weather causes higher relative humidity in the air and dung crust formation is slowed down, thus resulting in higher survival rates for the eggs.

Sphaeroceridae eggs are ovipositied on the surface of the dung and would therefore be extremely susceptible to desiccation whereas the larvae are able to move to moist areas. These observations are in general agreement with the findings of Wang (1964) who also found that desiccation and subsequent formation of a crust on the surface of the medium was accompanied by shrinkage of eggs and termination of development. Rohacèk (1983) showed that eggs of Sphaeroceridae are specially adapted for oviposition in liquid excrement because of their long respiratory horns. Furthermore Vogt & Woodburn (1980) found that at low humidities, some *Lucilia cuprina* (Wiedemann) eggs contained active larvae, many of which hatched after being flooded with water. They suggested that egg mortality at extremely low humidities stemmed from the inability of larvae to rupture the chorion (Vogt & Woodburn, 1980). However, Davies (1950) mentioned that shape changes in the chorion when eggs were shrinking, rather than hardening, were responsible for hatching difficulties of *L. sericata* and other blow fly species at low humidities. The fact that the duration of the egg stage is the shortest of the three immature stages in the life cycle of the Sphaeroceridae could minimize the effect of desiccation to a degree. Furthermore Sphaeroceridae females of both species failed to

oviposit in dry dung, as was observed during the execution of these experiments. The majority of eggs were deposited in dung with moisture content of 60% to 80%.

Extremely high moisture contents also had a negative effect on eggs, because under laboratory conditions, fewer eggs hatched on dung of high moisture content. This could be attributed to the fact that the eggs suffocated when they were fully submerged in water. This is also in accordance with findings by Hughes (1979), that showed that bush-fly eggs in Australia were adversely affected by inundation during periods of heavy rainfall. Karter *et al.* (1992), who studied the influence of abiotic factors on the eggs and larvae of the reindeer warble fly, *Hypoderma tarandi* (Linnaeus) (Hypodermatidae), found that eggs held at high moisture content under laboratory conditions showed lower viability and require a longer time to hatch relative to eggs held at lower moisture content. In statistical comparisons of egg hatching of the two species by using a t-test, results showed that at the lower moisture content (70% and lower), *C. hirtula* eggs were significantly better adapted to drier conditions than those of *C. vagans*. On the other hand the survival of *C. vagans* eggs was significantly better than those of *C. hirtula* at higher moisture content of 80% - 100%. This could be one of the contributing factors to *C. vagans* being the predominant species at the feedlot where conditions during the hot summer months are frequently extremely wet. These results furthermore demonstrated that extremely wet areas at the feedlot such as those around water troughs and dams were not conducive to egg development and hatching, and should therefore not require any additional chemical treatment for fly control.

4.3.2 Development of larvae

Larval development times of both *C. vagans* and *C. hirtula* were affected by dung moisture content from 40% up to 80% (Fig. 4.3). For *C. vagans* the shortest development time was 4.0 ± 0.2 days at 80% moisture content and *C. hirtula* showed development times of 4.0 ± 0.25 days at all the moisture contents from 80% and above

(Fig. 4.3). The longest development times, 7.0 ± 0.4 days for *C. vagans* and 6.5 ± 0.39 days for *C. hirtula*, were manifested at 40% moisture content (Fig. 4.3).

The development time of the larval stages of both species were plotted against moisture content and a good exponential relationship was shown to exist for both *C. vagans* (r = 0.96) and *C. hirtula* (r = 0.98) (Fig. 4.3). An increase in development time as moisture content decreased seemed to be the general trend among the immature stages of Sphaeroceridae because both the eggs and larvae followed the same trend towards the lower moisture contents of the range.

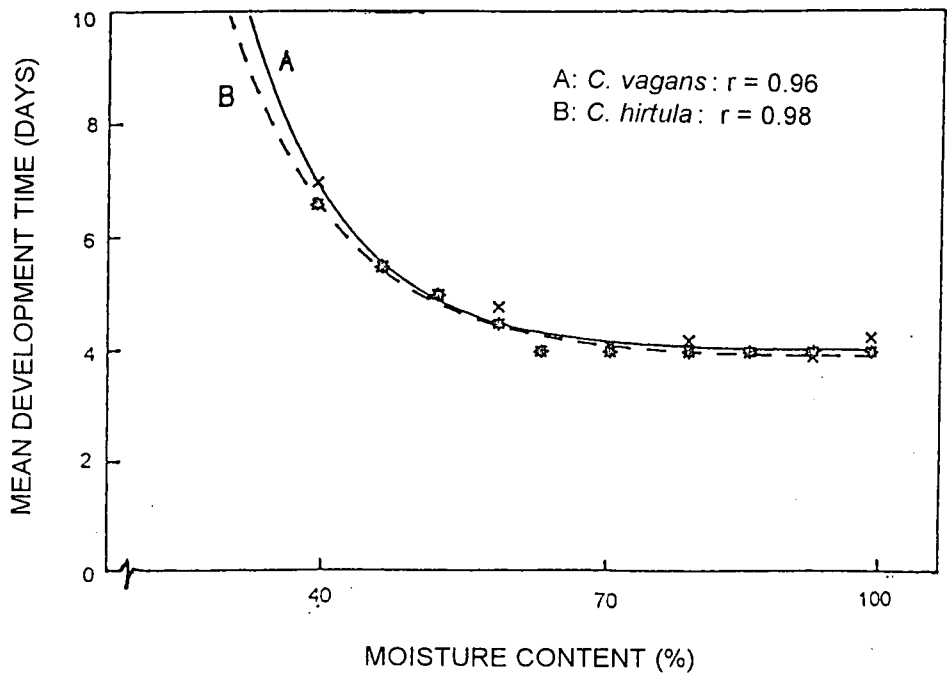


Figure 4.3: The exponential relationship between development time and moisture content for the larval stages of *Coproica vagans* and *Coproica hirtula*.

Based on analysis of variance ($F_{98;6}$=41.05), it was shown that for *C. vagans*, significant differences ($P<0.05$) in larval development times occurred (Table A4.5). Tukey's test ($Q_{0.05}$=20.52) showed that larval development at 40% and 50% moisture content took significantly longer than at the other treatments (Fig. A4.5). Significant differences were

also shown between 40% and 50% moisture content, while larval development at 60% and 70% proved to be significantly longer than at the higher moisture contents of 80% to 100%. For *C. hirtula*, analysis of variance ($F_{98;6}$=51.35) also showed significant differences ($P<0.05$) in larval development time between the different moisture contents (Table A4.6). Tukey's test ($Q_{0.05}$=29.65) similarly showed that larval development took significantly longer at 40%, 50% and 60% moisture content compared to the rearing media with higher moisture content. At 70% moisture content, development of *C. hirtula* larvae was significantly longer compared to the higher moisture contents at 80% and above, while larval development times at 40%, 50% and 60% moisture content also differed significantly from one another (Fig. A4.6). No significant differences existed in the development times of the larvae between 80% moisture content and above for either of the two species. By performing a t-test on the data, no significant differences ($P>0.05$) were shown between the development times of *C. vagans* and *C. hirtula* larvae at moisture contents from 50% - 60%, as well as from 80% - 90%. Significant differences ($P<0.05$) in larval development times between the two species could only be detected at 40%, 70% and 100% moisture content (Table A4.17).

Coproica vagans and *C. hirtula* larvae survived at all the different treatments. However, the best survival for *C. vagans* was 68 ± 8.1% and for *C. hirtula* 70 ± 8.2%, both at 90% moisture content. A steady decrease in percentage survival occurred towards the lower extreme of the moisture content range for both species. The lowest percentage survival for *C. vagans* was 7.0 ± 0.83% and 6.0 ± 0.79% for *C. hirtula*, both at 40% moisture content (Fig. 4.4).

With analysis of variance ($F_{98;6}$=22.77) significant differences ($P<0.05$) in survival of *C. vagans* larvae were shown (Table A4.7). With Tukey's test ($Q_{0.05}$=14.28) it was found that significant differences occurred in the survival of larvae between the lower moisture contents below 70% and the higher moisture contents above 80% (Fig. A4.7). Larval survival of *C. vagans* at 40% moisture content was significantly lower than the survival

at all other moisture contents. No significant differences in larval survival occurred between 60% and 70% moisture content or between 90% and 100% moisture content (Fig. A4.7). In the case of *C. hirtula*, significant differences ($P<0.05$) in larval survival rates were also shown with analysis of variance ($F_{98;6}=43.79$) (Table A4.8). Tukey's test ($Q_{0.05}=25.88$) indicated that the significant differences in larval survival rates were between 40%, 50% and the rest of the moisture contents (Fig. A4.8). The larval survival rates at the higher moisture contents (80% - 100%) also differed significantly from those at 60% and 70% moisture content. However, no significant differences in *C. hirtula* larval survival were found between 60% and 70% moisture content, between 80% and 90% moisture content or between 80% and 100% moisture content (Fig. A4.8). Furthermore a t-test that was done showed that significant differences ($P<0.05$) in larval survival existed between that of *C. vagans* and *C. hirtula* at all the moisture contents (Table A4.18).

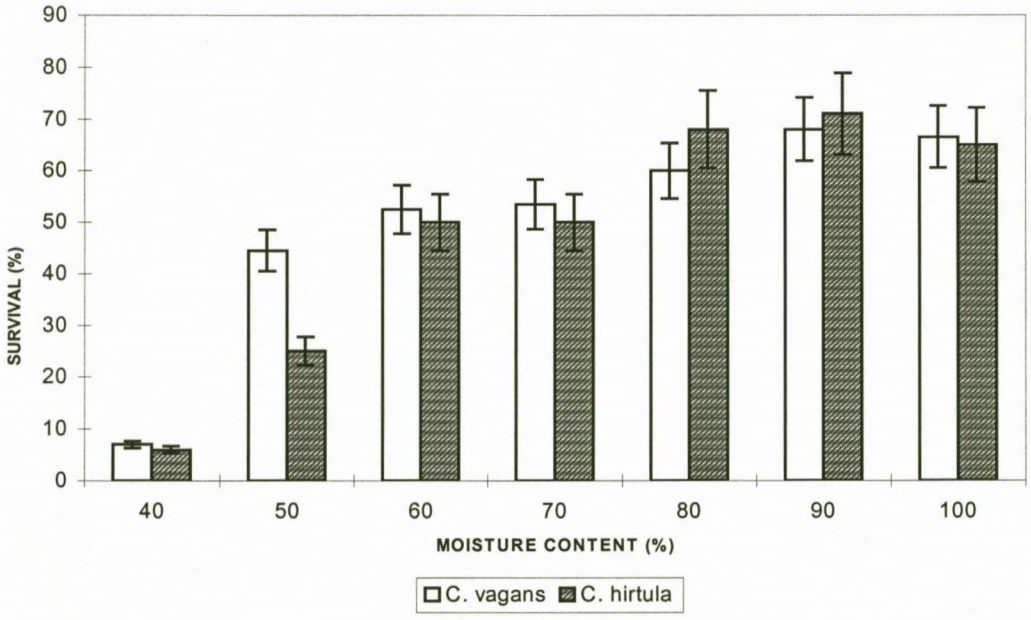


Figure 4.4: The percentage larval survival of *Coproica vagans* and *Coproica hirtula* at different constant moisture content.

Sphaeroceridae larvae are most dependent on the availability of moist dung simply because they rely on it as their only food resource. As in the case of the eggs, results again showed that a decrease in dung moisture content caused an increase in development time, which corresponds with findings of Buxton (1936). He stated that in many insect species, larval development is accelerated at high humidities, while other stages are little affected, although in some insects the relationship between humidity and velocity of development is more complex (Buxton, 1936). There are other fly species, particularly those that normally live in dry places, in which development rates appear to be quite unaffected by humidity, *e.g. Glossina* sp. (Buxton, 1936). In the case of Sphaeroceridae, larval development times only showed increases when moisture content dropped to below 80%. This retardation of fly larval development at low humidities has been analysed by Madge (1956) in terms of water loss during exposure to different humidities. The results were interpreted as indicating a reduction in the rate of metabolism as a result of the decrease in water content. In addition to affecting the speed with which development stages were completed, humidity also affected the proportion of individuals that complete development (Madge, 1956).

Results in this study showed that larvae of *C. vagans* and *C. hirtula* were extremely sensitive to lower humidities because at 40% moisture content, only between 6% and 7% of the larvae survived. At these lower moisture contents, most of the larvae died before reaching the pupal stage, and even when the larvae managed to develop to the pupal stage, emerging flies were weak and died within two to three days. These results are in general agreement with those in the literature, *e.g.* Davidson (1937) found that when dung dried out too much, it became unfavourable for the developing larvae of the Australian buffalo fly. According to Hammer (1941), *E. nigerrima* (Sphaeroceridae) died in less than 90 minutes at ordinary air temperature of 25°C and relative humidity of 50% in Denmark, and therefore tend to occur inside the dung mass. Meola (1964) stated that high humidity tended to be more favourable than low humidity, specifically for the larval stages in many insects. Mohr (1943) also found that water content of manure

could become a limiting factor for larvae of face flies if the dung became too dry for feeding. Valiela (1974), on the other hand, stated that the clustering behaviour of filter feeding face fly larvae within any one pat, caused ceaseless churning of the substrate by the aggregated larvae that resulted in a notable increase in the fluidity of the dung. Thus he maintained that the low water content of dung could hardly act as a factor limiting food availability for face flies (Valiela, 1974). *Coproica vagans* and *C. hirtula* larvae do not aggregate in dung in the same manner probably because of their smaller size and are thus unable to create favourable moisture conditions in the dung. This could explain their sensitivity to drying dung and the subsequent increase in mortality rates recorded for Sphaeroceridae larvae feeding on dung with moisture contents below 80%.

At the end of the larval stage, it appeared as if the Sphaeroceridae pupae that were formed at very low moisture contents (40% - 50%) appeared smaller and lighter in colour compared to those that were formed at 80% - 90% moisture content, although pupal size was not measured. This is in accordance with the findings of Depner (1961), who found that horn fly larvae in the USA died or formed small, nearly transparent pupae whenever the droppings dried out before larval development was completed. These small pupae resulted in the production of small adults that were only half the normal size (Depner, 1961). Muirhead-Thomsen (1988) found that relatively small reductions in the moisture content of dung pats, from 80% to 70%, rendered the dung virtually uninhabitable for the larvae of the Australian bush fly *M. vetustissima*. Although larvae of *C. vagans* and *C. hirtula* also showed an increase in sensitivity towards lower moisture contents, they were not as sensitive as *M. vetustissima*, because their survival in dung at 60% moisture content for example was between 50% and 53%. The survival of Sphaeroceridae larvae in the current study was in accordance with the findings of Bruno *et al.* (1994) who conducted a survey of synanthropic flies and their predators that breed in poultry manure accumulating at poultry farms in the state of Sao Paulo. They maintained that larvae required high levels of humidity and there were severe mortality rates when manure moisture content dropped from an optimal level of

55-80% to less than 30%. At the latter figure, no larval development took place (Bruno *et al.*, 1994).

At very high moisture content (*e.g.* 100%), larval survival was still above 60%, although a decrease in survival was shown in the case of *C. hirtula* when compared to larval survival at 90% moisture content. This phenomenon also occurred in the case of the eggs, which would therefore indicated that larval mortality would increase at moisture contents above the optimum level of 90%. This could also be as a result of nutrient dilution of the dung at high moisture content, which would then cause additional mortality among fly larvae, as was suggested by Hogsette (1996).

4.3.3 Development of pupae

The development times of both *C. vagans* and *C. hirtula* pupae also varied as the moisture content of the dung decreased below a moisture content of 100% (Fig. 4.5). In the case of *C. vagans*, the shortest development time for the pupae was 5.2 ± 0.6 days at both 90% and 100% moisture content, while for *C. hirtula* pupae, the shortest development time was also 5.0 ± 0.7 days, also at 100% moisture content. The longest development times were 9.0 ± 0.8 days and 9.0 ± 0.7 days for *C. vagans* and *C. hirtula* respectively, both at 40% moisture content (Fig. 4.5).

When plotting the development time of the pupal stages of both species against moisture content, a good exponential relationship was shown to exist for both *C. vagans* ($r = 0.96$) and *C. hirtula* ($r = 0.96$) - (Fig. 4.5).

For *C. vagans*, analysis of variance ($F_{77;6}=35.40$) showed that significant differences ($P<0.05$) in pupal development times occurred (Table A4.9). Tukey's test ($Q_{0.05}=19.87$) indicated that it took significantly longer to complete the pupal stage at moisture contents of 40% to 60% than at higher moisture treatments above 60% (Fig. A4.9). No

significant differences in pupal development times were recorded between 70% and 80% moisture content or between 90% and 100% moisture content (Fig. A4.9). In the case of *C. hirtula*, significant differences ($P<0.05$) in the development time of the pupae were also shown with analysis of variance ($F_{77;6}=28.42$) (Table A4.10). Tukey's test ($Q_{0.05}=13.31$) indicated that the development of the pupae at 40% and 50% moisture content of the dung was significantly longer than at the higher moisture contents above 50% (Fig. A4.10). No significant differences were found between 70%, 80% or 90% moisture content, although pupal development at 100% moisture content was significantly shorter compared to the lower moisture contents (Fig. A4.10). A t-test was also done to compare the mean development times of *C. vagans* and *C. hirtula* pupae with each other. These statistical results showed that significant differences ($P<0.05$) existed in pupal development times between the two species at all the different moisture contents that were tested, except at 40%, 60% and 70% moisture content (Table A4.17).

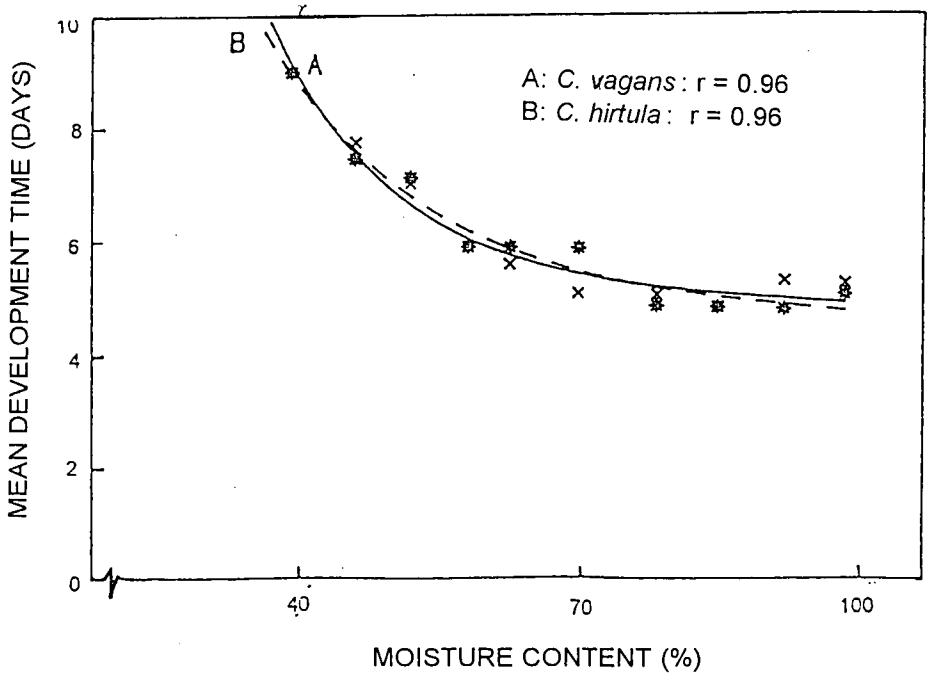


Figure 4.5: The exponential relationship between the mean development time of the pupal stages of *Coproica vagans* and *Coproica hirtula* and moisture content.

The highest percentage pupal survival was at 70% moisture content where 86 ± 10.1% of *C. vagans* and 87 ± 9.7% of *C. hirtula* pupae reached adulthood (Fig. 4.6). In both cases the survival percentages steadily decreased towards the lower and higher extreme of the moisture content range (Fig. 4.6). The lowest survival rate of the pupae occurred at 40% moisture content, although this was still relatively high (*viz.* 54 ± 6.5% for *C. vagans* and 45 ± 5.9% for *C. hirtula* respectively) (Figs 4.6) compared to the egg and larval stages.

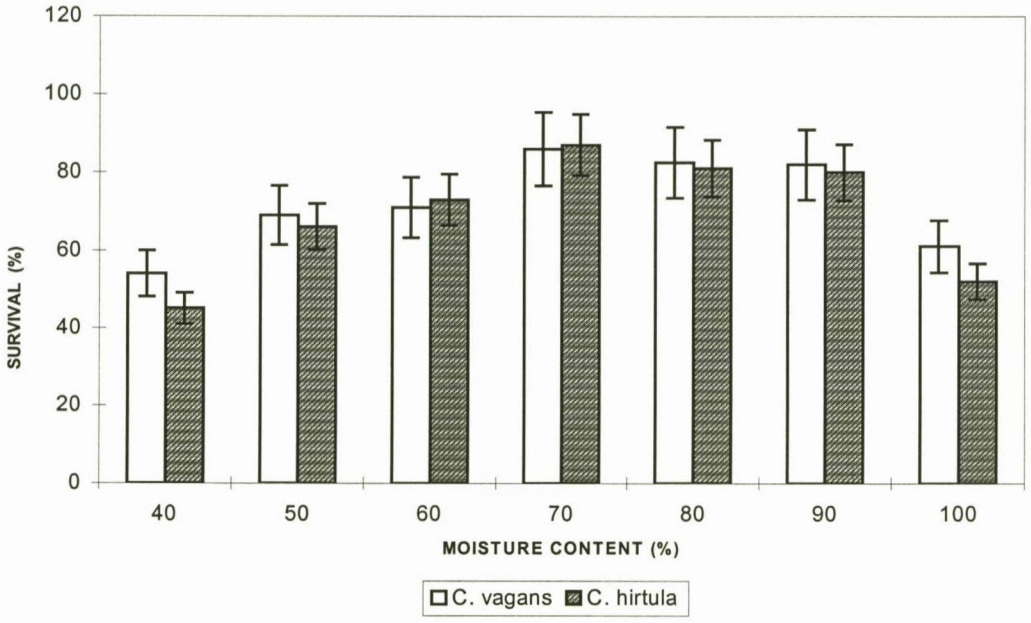


Figure 4.6: The percentage survival of pupae of *Coproica vagans* and *Coproica hirtula* at different constant moisture content.

Based on analysis of variance ($F_{77;6}$=5.92), significant differences ($P<0.05$) in the percentage survival of pupae between the different moisture treatments were shown for *C. vagans* (Table A4.11). Tukey's test ($Q_{0.05}$=1.59) showed that significant differences in survival of *C. vagans* pupae occurred between the 40% moisture content treatment and the other higher moisture contents above 50% (Fig. A4.11). No significant differences in *C. vagans* pupal survival were shown between 50% and 60% moisture content or between values at 80% and 90% moisture content. Pupal survival at 70% moisture

content was significantly higher than at all other moisture contents above or below 70% (Fig. A4.11). In the case of *C. hirtula*, analysis of variance ($F_{77;6}$=21.94) also indicated that significant differences ($P<0.05$) existed in the pupal survival between the different moisture contents that were tested (Table A4.12). Tukey's test ($Q_{0.05}$=9.35) showed that the significant differences were between the pupal survival rates at 40% and 70% and all other moisture contents (Fig. A4.12). No significant differences were found in *C. hirtula* pupal survival between 80% and 90% moisture content (Fig. A4.12). Significant differences ($P<0.05$) were also shown in pupal survival between *C. vagans* and *C. hirtula* at all the different moisture contents that were tested by using a t-test to compare the two species with each other (Table A4.18).

The results clearly indicated that development times of pupae increased at lower moisture contents, although not as much as in the case of the eggs and larvae. In exceptional cases where additional pupae had to be collected from the laboratory colonies to complete certain experiments, this may have influenced the results because the larvae in the laboratory colonies were kept at much higher moisture contents. However, this was only done at the lowest moisture content treatment (40%), and moisture contents from 50% and above all included pupae that were formed from larvae kept at similar moisture content.

Pupal survival of *C. vagans* and *C. hirtula* at the lowest moisture content tested was above 45% in both cases. This indicates that the pupal stage was the most tolerant to drier conditions, because at 40% moisture content, hatching percentages of *C. vagans* and *C. hirtula* eggs were only 1% and 11% respectively (Fig. 4.2), while the larval survival rates were only 7% and 6% respectively (Fig. 4.4). In natural dung pats Sphaeroceridae eggs are oviposited while dung is still wet and fresh, but as the dung pats become older and drier, its inhabitants need to adapt to these drier conditions to survive. By the time the flies reach the pupal stage, natural dung pats are already much drier, and in terms of natural selection, this could explain the ability of the Sphaeroceridae pupae to

tolerate such dry conditions better than the eggs or larvae. According to Hafez (1939), a pronounced decrease in water content of dung pats occurred as time passed. Valiela (1974) also showed in studies with the face fly, *M. autumnalis* in the USA, that natural dung pats older than six days showed a significant decrease in water content. However, he emphasized that in natural pats this does not cause any particular problem, since no drastic changes occurred during the short time that face flies are present in the dung (Valiela, 1974). In general, flies with longer development cycles showed greater resistance to low moisture content in the dung than flies with short development cycles (Hammer, 1941). Barth *et al.* (1995) showed that small differences in moisture content of only 1 - 2 %, that may not be distinguishable by visual inspection, have an impact on the development of Diptera, Coleoptera and earthworms in dung, as well as on dung degradation. In contrast to natural dung pats, conditions at the feedlot are constantly wet because of the large amounts of fresh cattle dung and urine that are excreted daily in a very small area and also because of higher rainfall during summer. Moisture content therefore has no limiting effect on the development and survival of Sphaeroceridae at feedlots, and this could be one of the reasons why Sphaeroceridae has become a serious problem at South African feedlots and not in other parts of the world. Pupal survival at 90% moisture content was also above 75%, indicating that even the pupae are well adapted for these wet conditions at the feedlot.

The current study results also corresponded with the findings by Davidson (1937), who stated that pupae of the Australian buffalo-fly required less moisture in their environment than developing larvae. Mohr (1943) found that third instar Diptera larvae that are ready to pupate normally move to drier areas in the dung pat, or mostly into the soil beneath the pat where pupation then takes place. This could explain the occurrence of most Sphaeroceridae pupae in the drier dung under the peripheral fences of the feedlot camps. Milward-de Azavedo *et al.* (1992) attempted to verify the influence of soil humidity on pupal duration and viability, emergence rhythm and survival of *Cochliomyia* sp. adults under laboratory conditions. This was done on the basis of water

retention curves and it was found that the duration of the pupal stage was the same at the higher humidities tested (above 70%), while most humid treatments resulted in higher adult percentages. Hammer (1941) found that desiccation of the soil surface will barely harm the pupae if the air humidity in the pores of the dung is near saturation. Even if the moisture content in these pores and cracks inside the dung is very low, the pupae would still survive (Hammer, 1941). Pupae are often found in such microhabitats, indicating that the larvae apparently migrated to well-aerated sites protected from complete desiccation (Hammer, 1941). Buxton (1936) published a record to this effect on *Glossina* sp. and found that even ground water content of 4% was sufficient for pupal survival. Based on the percentage pupae reaching adulthood at 40%, it is possible that some pupae could have survived at dung moisture contents below 40%. However, the critical minimum moisture content for Sphaeroceridae pupae was not determined because of the inability of eggs and larvae to develop and survive at such low moisture content. Total immature development also indicated that only between 0.025% and 0.12% of the eggs oviposited at 40% moisture content successfully developed to adulthood (see Fig. 4.11). No development of Sphaeroceridae at 30% moisture content would therefore be possible and it was decided to keep the moisture content range for these experiments between 40% and 100%.

Although pupal survival at 100% moisture content was above 60%; it was also observed that at such high moisture content, some pupae became mouldy, probably due to excess moisture in the medium. This may be one of the reasons for the lower pupal survival at the highest moisture content. The fact that pupae can survive fairly well at drier conditions, together with their resistance to lower temperatures (see Chapter 3 - 3.3.3), support the suggestion that the pupal stage might be the diapause phase during which the flies survive the colder, drier conditions that prevail at feedlots during winter. This is merely speculative, because all attempts to record quantitative data on pupae in dry feedlot dung during the winter were unsuccessful. Only one or two pupae were found per square metre.

4.3.4 Total immature development

As expected, the total development time of the immature stages showed the same tendency as that of the egg, larval and pupal stages, namely that an increase in development time occurred as the moisture content decreased below 100% moisture content (Fig. 4.7). In the case of *C. vagans*, the shortest development time was 11.7 ± 0.9 days, and for *C. hirtula*, the development time was 11.6 ± 0.9 days, both occurring at 90% and 100% moisture content. For *C. vagans* and *C. hirtula*, the longest development times were 22 ± 1.3 and 21 ± 1.1 days respectively at 40% moisture content (Fig. 4.7).

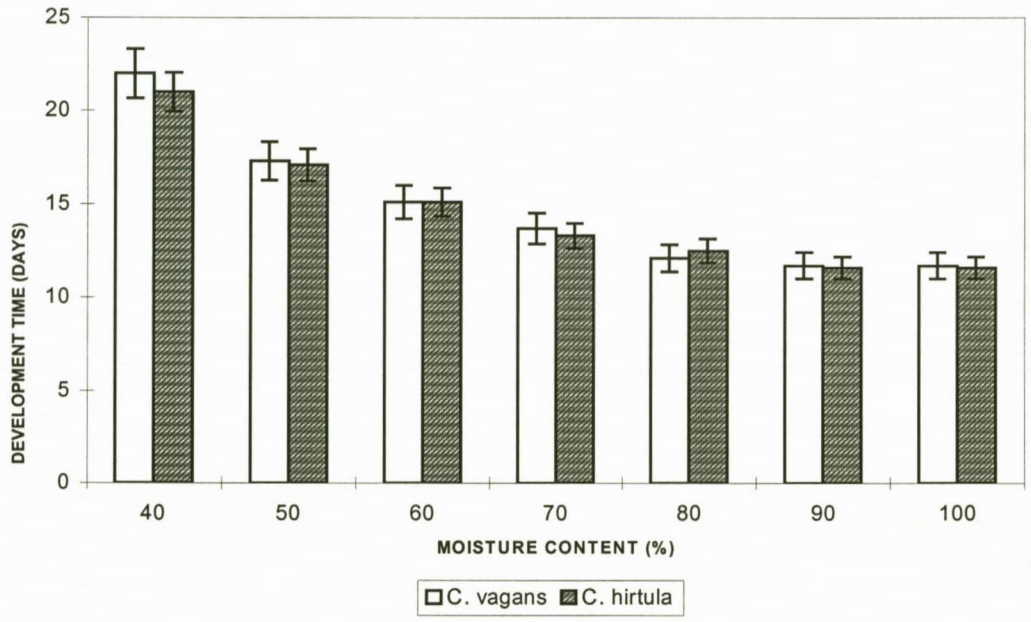


Figure 4.7: Total development times of immature stages of *Coproica vagans* and *Coproica hirtula* at different constant moisture content.

More *C. vagans* and *C. hirtula* adults were produced from the eggs that were oviposited and allowed to develop to adulthood at 90% moisture content than at higher or lower moisture contents (Fig. 4.8). For *C. vagans* an average of 35 ± 3.1% of eggs produced reached adulthood at 90% moisture content and for *C. hirtula* this figure was 39.8 ±

3.8%. At a moisture content of 40%, only 0.025 ± 0.01% of the *C. vagans* eggs and 0.12 ± 0.01% of *C. hirtula* eggs reached adulthood. It was also noted that at moisture contents of 60%, 80% and 90%, significantly more ($P<0.05$) *C. hirtula* adults were produced than *C. vagans* adults (Fig. 4.8).

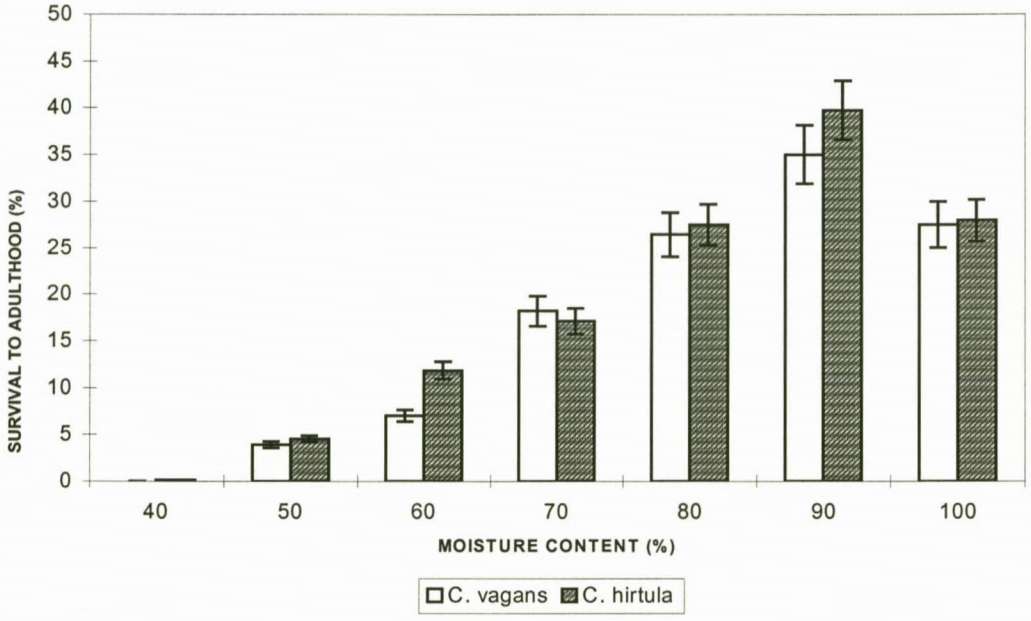


Figure 4.8: The percentage eggs that reached adulthood for both *Coproica vagans* and *Coproica hirtula* at different moisture content.

With analysis of variance ($F_{98;6}=21.38$), significant differences ($P<0.05$) in the overall immature development were shown for *C. vagans* (Table A4.13). Tukey's test ($Q_{0.05}=12.35$) indicated that significant differences existed in the number of adults that were produced between all the different moisture contents, except between 80% and 100% (Fig. A4.13). The analysis of variance ($F_{98;6}=62.32$) for *C. hirtula* also indicated significant differences ($P<0.05$) in its total immature development time (Table A4.14). With the Tukey's test ($Q_{0.05}=31.33$) significant differences were shown between all the moisture treatments, except between the 80% and 100% dung moisture content (Fig. A4.14). A t-test was also used to compare the total survival of immature stages of *C.*

vagans and *C. hirtula* with each other at the different dung moisture contents. Significant differences ($P<0.05$) were shown at all the moisture contents except at 40% (Table A4.18).

4.3.5 Adult flies

A good linear relationship existed between moisture content of dung and survival time of adult flies for both *C. vagans* (r = 0.98) (Fig. 4.9) and *C. hirtula* (r = 0.97) in the laboratory (Fig. 4.10). Longevity of adult flies increased with an increase in moisture content. At 40% moisture content, the adult flies of *C. vagans* and *C. hirtula* survived for an average of 5.5 ± 0.4 days and 3.0 ± 0.25 days respectively, while at 100%, they survived up to 16.0 ± 1.2 days and 16.5 ± 1.4 days respectively (Fig. 4.9 & 4.10). The results furthermore showed that the longevity of *C. vagans* adults was better at the lower moisture contents (40% and 50%) than *C. hirtula*, while at the higher moisture contents (80% - 100%), *C. hirtula* adults survived longer.

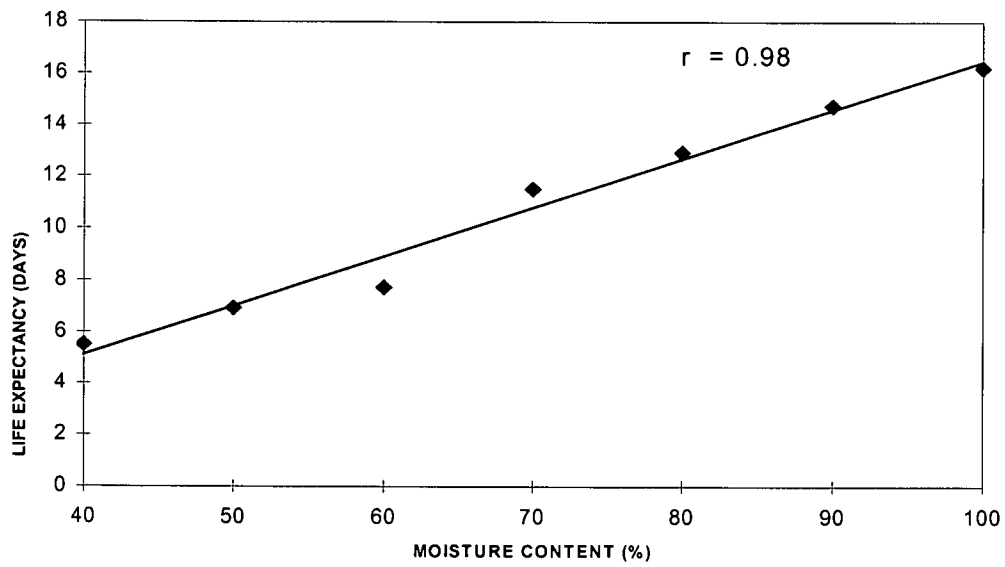


Figure 4.9: Longevity of adult *Coproica vagans* flies at different moisture content.

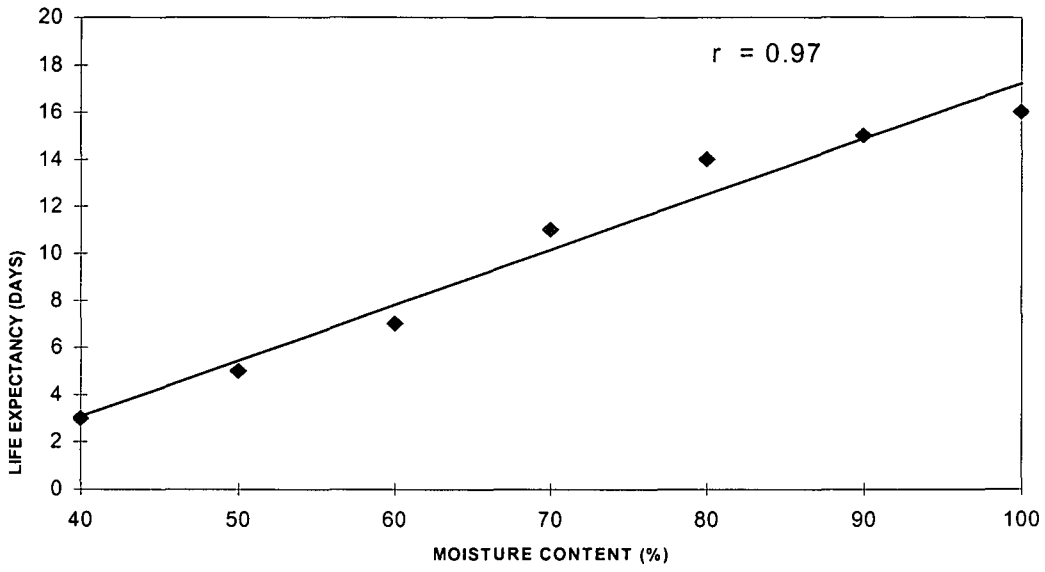


Figure 4.10: Longevity of adult *Coproica hirtula* flies at different moisture content.

With analysis of variance ($F_{63;6}$=19.41), significant differences (P<0.05) in the life expectancies between the different moisture treatments were shown for *C. vagans* adults (Table A4.15). With Tukey's test ($Q_{0.05}$=4.24) significant differences were shown in the life expectancies of *C. vagans* adults between all the different moisture contents from 40% to 100% (Fig. A4.15). In the case of *C. hirtula*, analysis of variance ($F_{63;6}$=64.92) also indicated that significant differences (P<0.05) existed in the adult life expectancies between the different moisture content that were tested (Table A4.16). Tukey's test ($Q_{0.05}$=22.93) showed that significant differences existed between the life expectancies at all the moisture contents tested in this experiment from 40% to 100% (Fig. A4.16).

Moisture is essential for the survival of adult flies because moist dung acts as a food resource. The results that were obtained indicated that if the dung medium became either too wet of too dry, it will have serious implications for the survival of adult flies. These findings corresponded with those of Roberts & Pitts (1971), who found that face fly populations in the USA were lower during periods of high relative humidities. Although the life strategies, habitat and feeding habits of tsetse flies differ completely from

Sphaeroceridae, Roberts & Pitts (1971) found that adult tsetse flies (*Glossina* sp.) were more active in dry than moist air. The movements of face flies also slowed down in dry air, but they were also less active at relative humidities above 80% (Wang, 1964). Above 90%, they appeared sluggish and weak and all feeding, mating and ovipositing ceased (Wang, 1964). Hogsette, (1996) also stated that the survival of adult house flies in Florida, USA was also severely reduced at low moisture content.

Although these experiments with Sphaeroceridae were all done in the laboratory under controlled conditions, it is important to remember that humidity is also important under natural field conditions. During hotter and drier seasons at the feedlots, swarms of adult Sphaeroceridae were observed at the wetter areas around water troughs and manure dams. This seems to be the general tendency among flies, because Meyer & Shultz (1990) also found large concentrations of house flies in moist areas near water troughs and in piled manure at Californian dairies. Edwards (1991) also found that the African bush fly, *Haematobia thirouxi* (Bezzi) for instance, could not use wildebeest dung when the moisture content was less than 10%. However, at moisture contents of 73% and above, the size and survival of African bush flies improved (Edwards, 1991). The moisture content of freshly voided cattle faeces is important with regard to colonization by fauna and the rate of degradation of dung pats (Barth *et al.*, 1995). Modassir (1993) studied seasonal abundance of three Sepsis species, namely *Sepsis nitens* (Fabricius), *Sepsis albopunctata* (Fabricius), and *Australosepsis niveipennis* (Becker) in relation to environmental factors and found that humidity and cloudiness were both factors that influenced the abundance and seasonal distribution of these flies.

In an attempt to comprehend the effect of moisture on the survival of adult Sphaeroceridae flies, a general discussion on some physiological aspects is relevant at this stage. To survive, insects must maintain their water balance between certain well-defined limits. They must, under different environmental conditions, strike a balance between losses and gains in such a way that their water reserves do not become critically

depleted, nor do the tissues become hydrated beyond a certain level (Lee & Denlinger, 1985b). In some insects, at least, regulation of spiracular and excretory moisture losses may play an important role in achieving this objective. The general level of cuticular permeability determines the range of environmental conditions under which such regulatory powers are likely to be of avail. If the integument is very permeable, regulation may be effective at the humid end of the scale, but exposure to very dry conditions are likely to prove fatal, and if the integument is relatively impermeable, regulatory powers may sustain the animal even over the drier parts of the humidity range (Bursell, 1958). According to Johnson (1940), the rate at which water is lost at lower humidities is greater and therefore the lower critical levels of water content will be reached sooner.

The use of reconstituted dung instead of fresh dung was essential for this study to create and maintain the desired moisture content in the dung. According to Bay *et al.* (1969) statistical analysis showed no significant difference in pupal weight or percentage adult emergence between bioassays conducted with fresh bovine faeces and freeze-dried faeces reconstituted with distilled water. Oviposition also took place in reconstituted dung if fresh dung was not available (Bay *et al.*, 1969). The fact that these experiments were done in small cups and vials probably caused the dung to retain more water than it would under most field conditions. However, it was still necessary to add small amounts of water, with the same temperature as the dung, to the rearing medium daily to compensate for the moisture loss through evaporation. Fredeen & Glen (1970) also added water to the medium to maintain the moisture content at a constant level in their experiments with *L. caenosa*.

In conclusion, the data have indicated that humidity may influence the reproductive potential of *C. vagans* and *C. hirtula* by not only affecting the development rate but also the survival of all stages. Both too much and too little moisture has a negative effect on development and survival of sphaerocerid flies in laboratory experiments as well as at

feedlots. Observations made at the feedlot showed that Sphaeroceridae flies avoided areas that were either too dry or too wet, and occurred mainly on fresh dung near the peripheral fences of the camps or at the feeding troughs. The results clearly showed that both species prefer a moist habitat. Sphaeroceridae constitute a serious problem at all the feedlots in South Africa, and during the summer months from December to March, most feedlots record high rainfall figures. This would then result in the creation of an ideal moist habitat for Sphaeroceridae to develop. This data provided good insight into the moisture preferences of Sphaeroceridae, and by also taking meteorological data into account, it is now possible to predict outbreaks of Sphaeroceridae at feedlots that would in turn render it possible to implement an integrated control program at cattle feedlots.

4.4 APPENDIX

Table A4.1: Analysis of variance of the development time for the eggs of *Coproica vagans* at different moisture content.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	106.485714	6	17.747619	64.6300578	4.8844E-25	2.24640928
Error	17.3	63	0.27460317			
Total	123.785714	69				

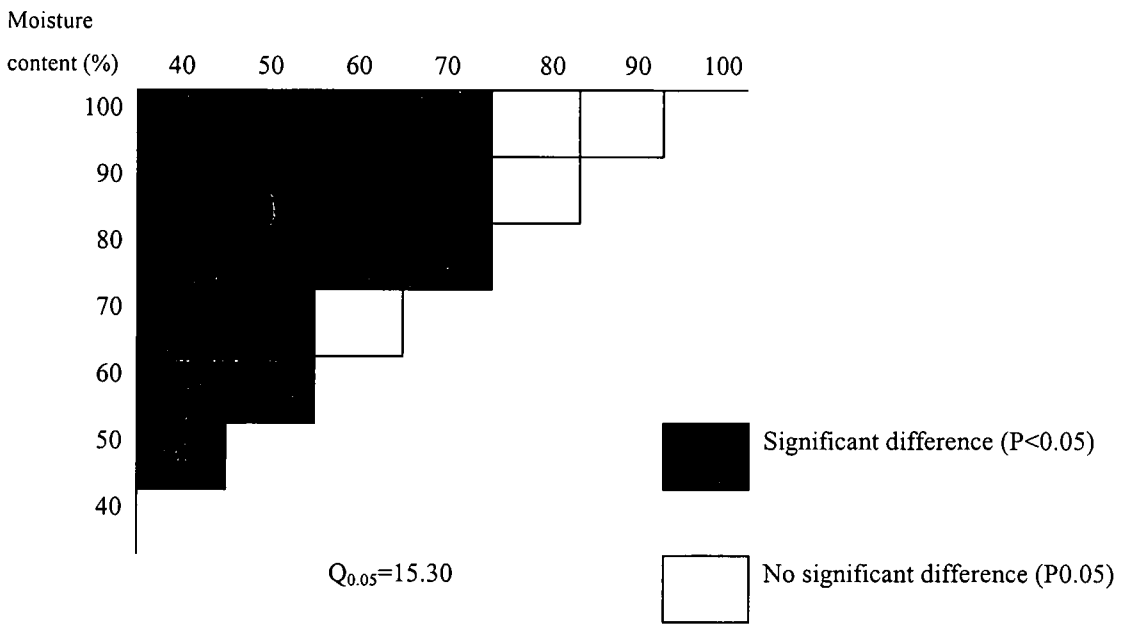


Figure A4.1: A schematic presentation of the significant differences in development time of *Coproica vagans* eggs at different moisture content.

Table A4.2: Analysis of variance of the development time for the eggs of *Coproica hirtula* at different moisture content.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	76.5428571	6	12.7571429	51.7181467	1.7372E-22	2.24640928
Error	15.54	63	0.24666667			
Total	92.0828571	69				

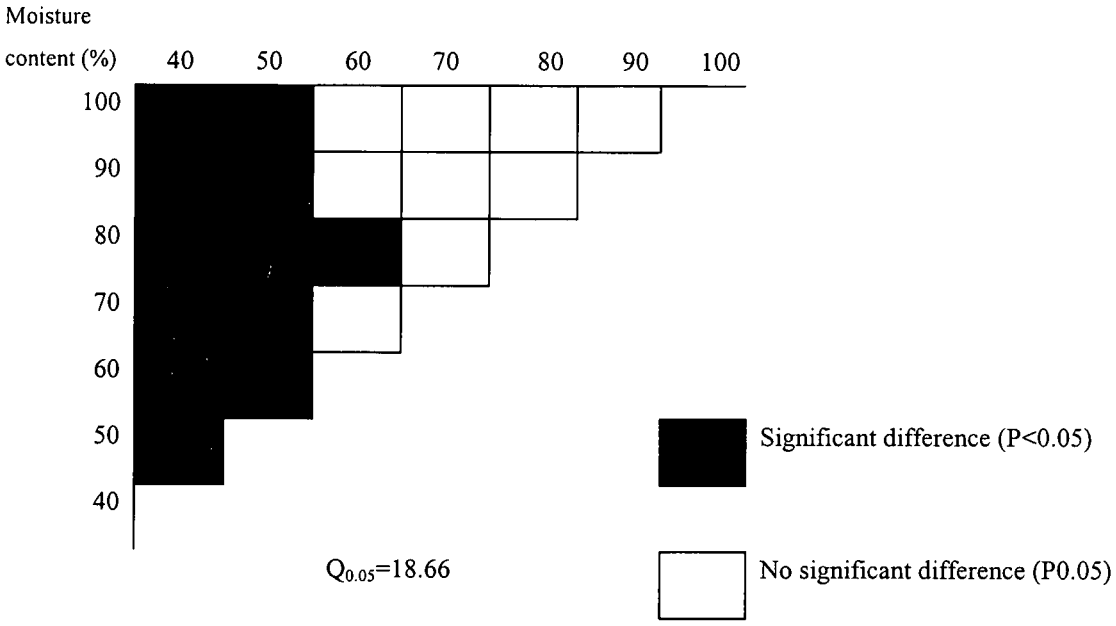


Figure A4.2: A schematic presentation of the significant differences in development time of *Coproica hirtula* eggs at different moisture content.

Table A4.3: Analysis of variance of the percentage hatching of the eggs of *Coproica vagans* at different moisture content.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	38853.3714	6	6475.5619	80.9332831	1.0619E-27	2.24640928
Error	5040.7	63	80.0111111			
Total	43894.0714	69				

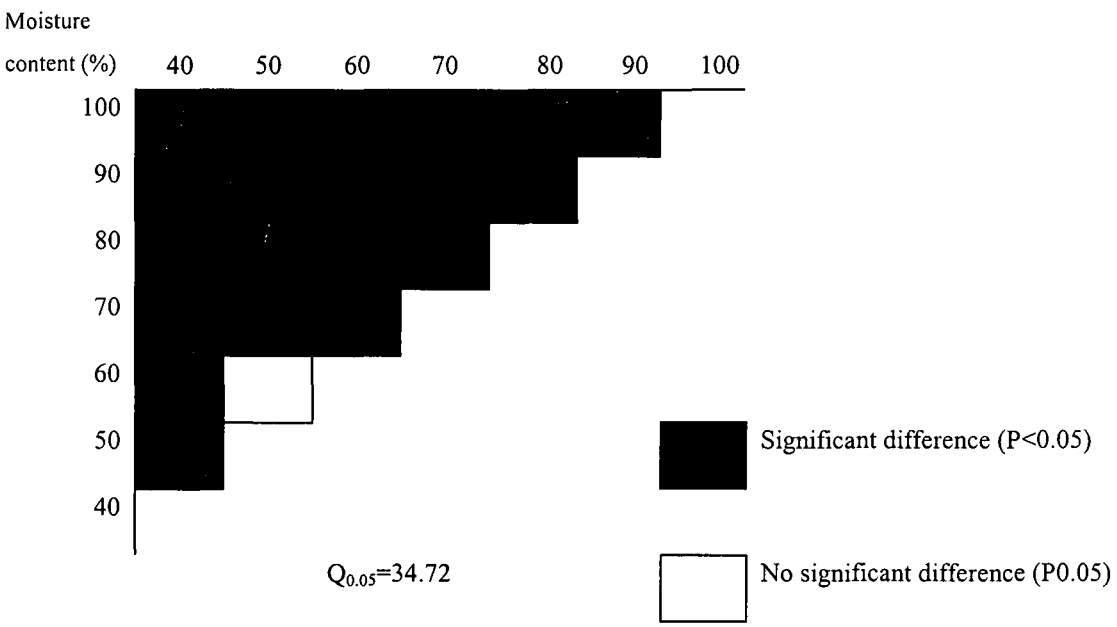


Figure A4.3: A schematic presentation of the significant differences in hatching of *Coproica vagans* eggs at different moisture content.

Table A4.4: Analysis of variance of the percentage hatching of the eggs of *Coproica hirtula* at different moisture content.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	22159.2857	6	6693.21429	21.77562	3.7448E-40	2.24640928
Error	1068.5	63	86.9603175			
Total	23227.7857	69				

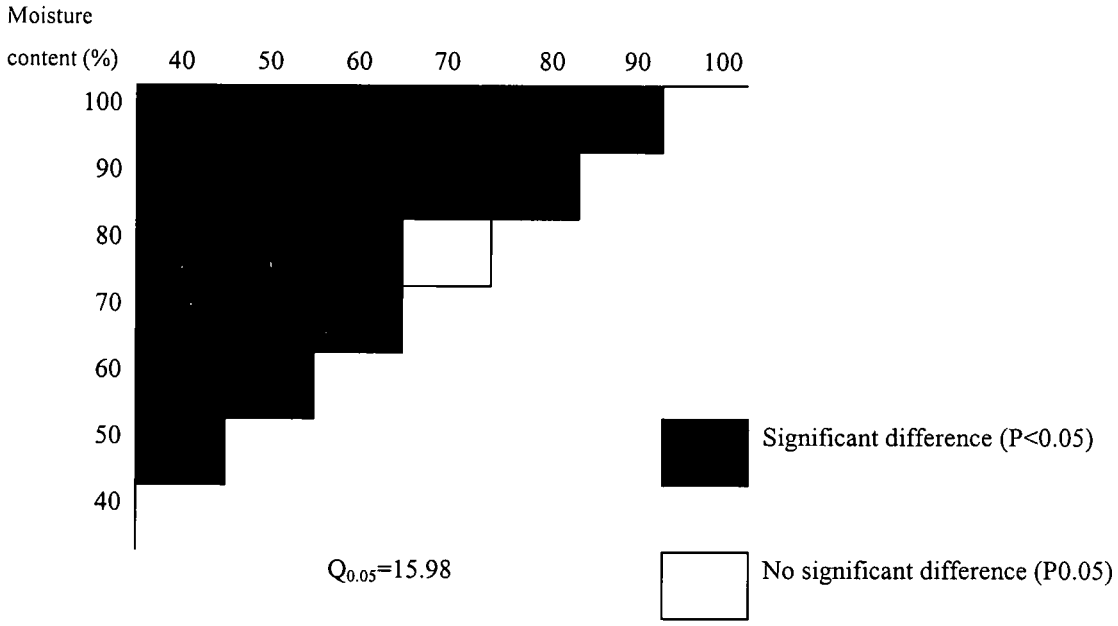


Figure A4.4: A schematic presentation of the significant differences in hatching of *Coproica hirtula* eggs at different moisture content.

Table A4.5: Analysis of variance of the development time for the larvae of *Coproica vagans* at different moisture content.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	68.7428571	6	11.4571429	41.0461538	1.439E-31	2.24640928
Error	6.5	98	0.1031746			
Total	75.2428571	104				

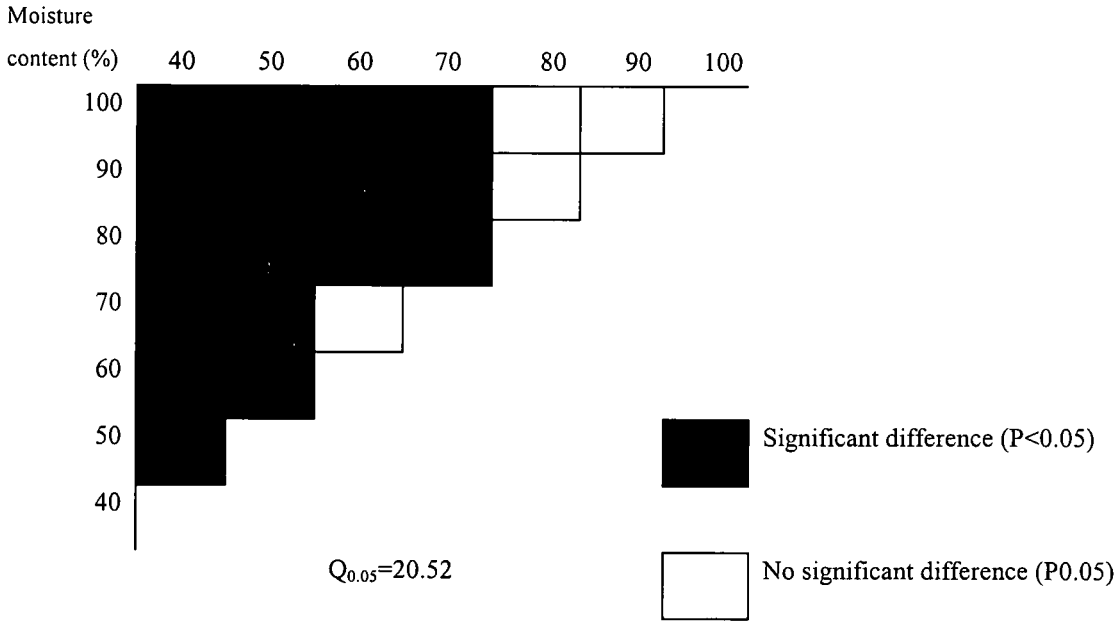


Figure A4.5: A schematic presentation of the significant differences in development time of *Coproica vagans* larvae at different moisture content.

Table A4.6: Analysis of variance of the development time for the larvae of *Coproica hirtula* at different moisture content.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	54.2857143	6	9.04761905	51.3461538	3.6448E-29	2.24640928
Error	6.24	98	0.09904762			
Total	60.5257143	104				

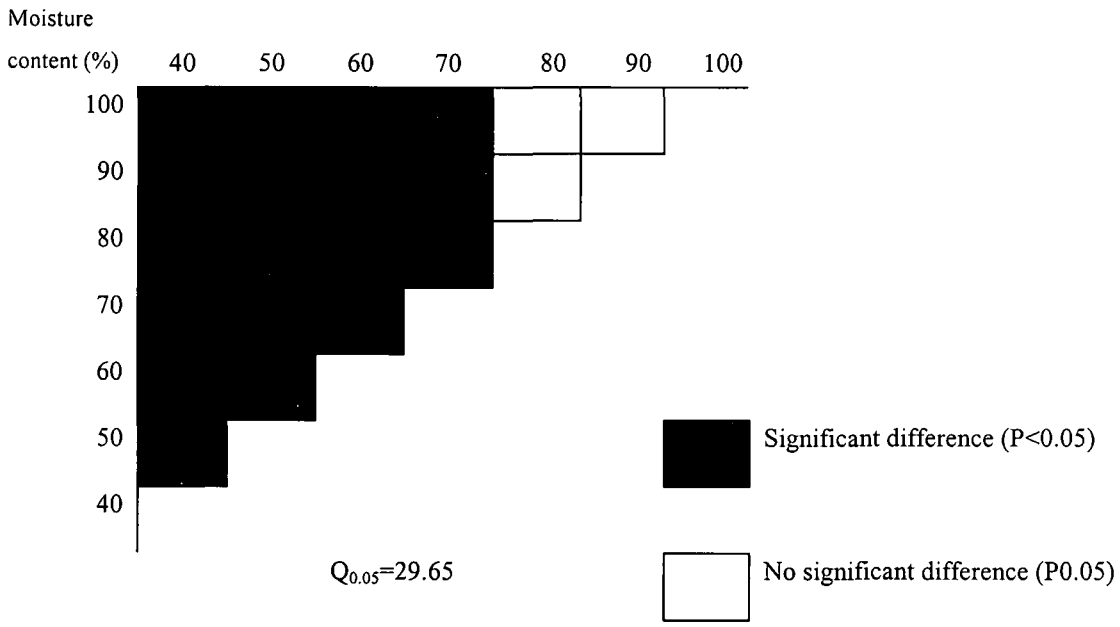


Figure A4.6: A schematic presentation of the significant differences in development time of *Coproica hirtula* larvae at different moisture content.

Table A4.7: Analysis of variance of the percentage survival of larvae of *Coproica vagans* at different moisture content.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	25503.5714	6	4250.59524	22.7662062	4.397E-14	2.24640928
Error	11762.5	98	186.706349			
Total	37266.0714	104				

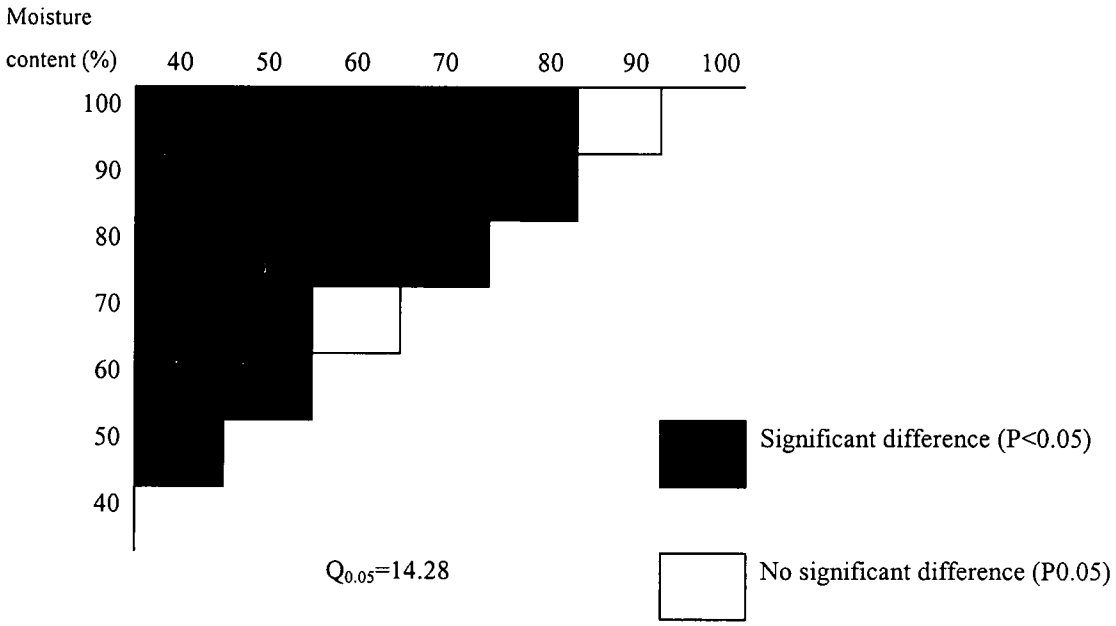


Figure A4.7: A schematic presentation of the significant differences in survival of *Coproica vagans* larvae at different moisture content.

Table A4.8: Analysis of variance of the percentage survival of larvae of *Coproica hirtula* at different moisture content.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	8223.57143	6	6370.59524	43.7913257	2.2675E-49	2.24640928
Error	216.5	98	14.547619			
Total	39140.0714	104				

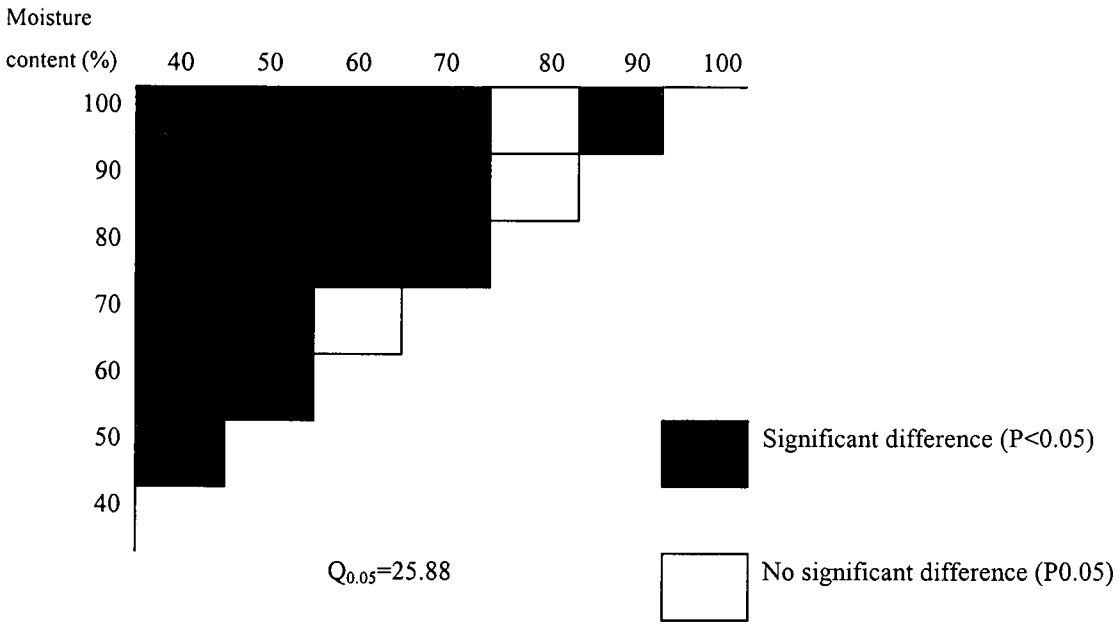


Figure A4.8: A schematic presentation of the significant differences in survival of *Coproica hirtula* larvae at different moisture content.

Table A4.9: Analysis of variance of the development time for the pupae of *Coproica vagans* at different moisture content.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	125.342857	6	20.8904762	35.4012346	4.7066E-34	2.24640928
Error	9.72	77	0.15428571			
Total	135.062857	83				

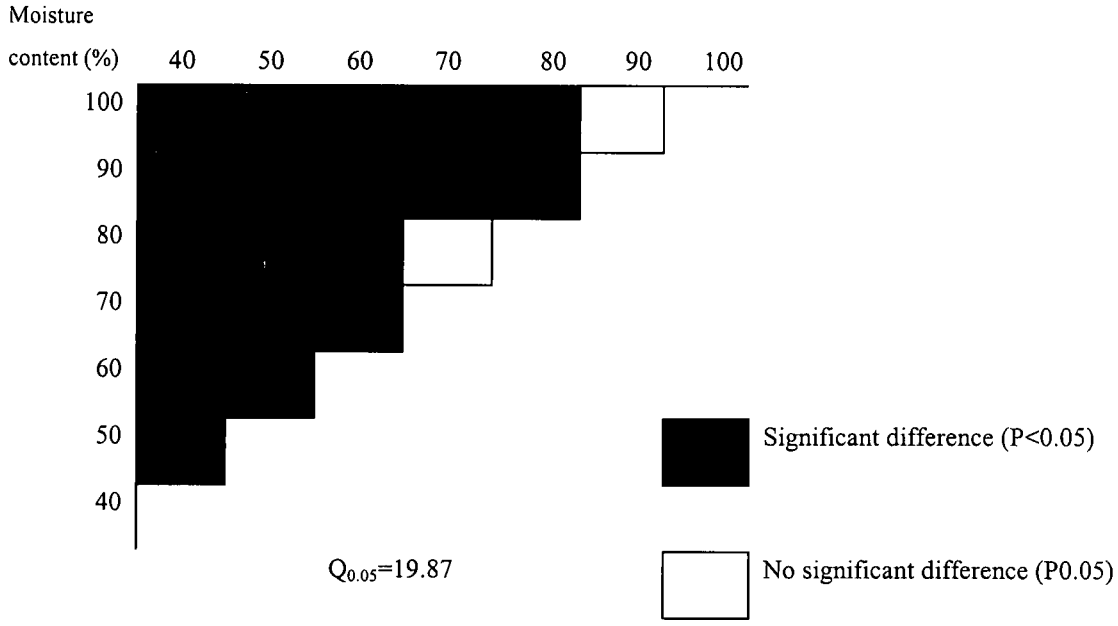


Figure A4.9: A schematic presentation of the significant differences in development time of *Coproica vagans* pupae at different moisture content.

Table A4.10: Analysis of variance of the development time for the pupae of *Coproica hirtula* at different moisture content.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	105.171429	6	17.5285714	28.4224599	4.4562E-30	2.24640928
Error	11.22	77	0.17809524			
Total	116.391429	83				

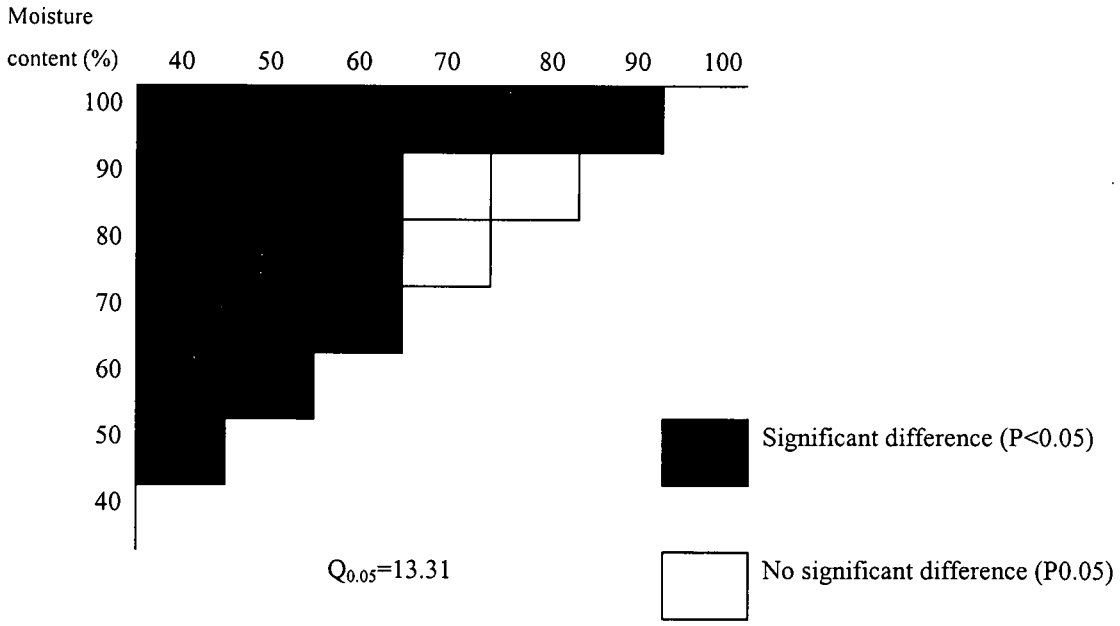


Figure A4.10: A schematic presentation of the significant differences in development time of *Coproica hirtula* pupae at different moisture content.

Table A4.11: Analysis of variance of the percentage survival of pupae of *Coproica vagans* at different moisture content.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	8045	6	1340.83333	5.91751313	6.0549E-05	2.24640928
Error	14275	77	226.587302			
Total	22320	83				

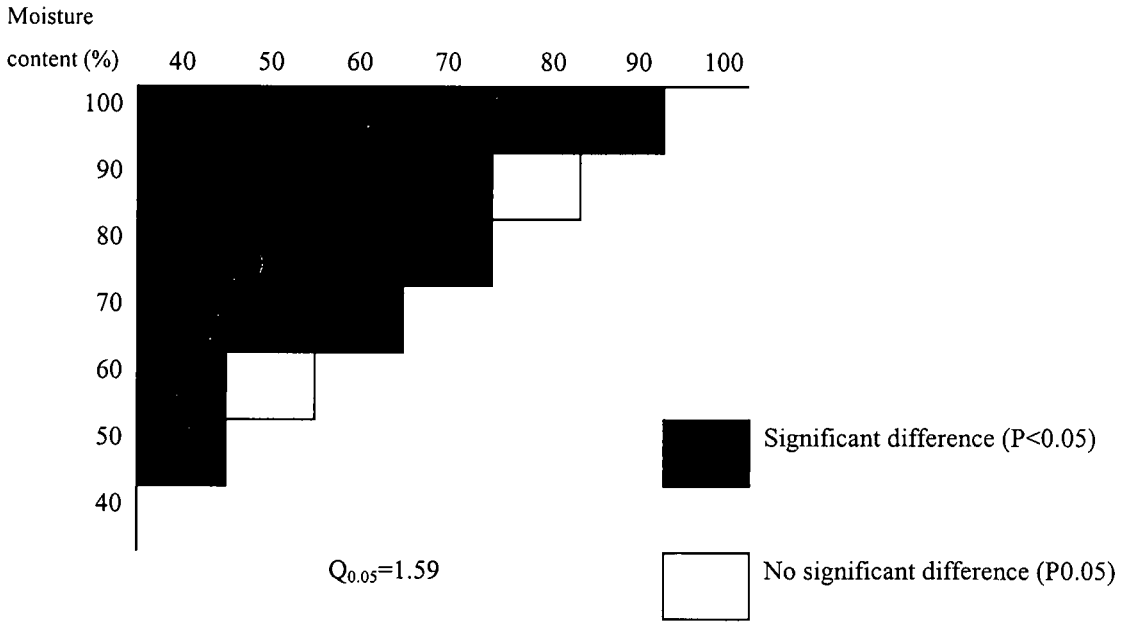


Figure A4.11: A schematic presentation of the significant differences in survival of *Coproica vagans* pupae at different moisture content.

Table A4.12: Analysis of variance of the percentage survival of pupae of *Coproica hirtula* at different moisture content.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	13768.8571	6	2294.80952	21.9448998	2.41E-14	2.23118946
Error	7320	77	104.571429			
Total	21088.8571	83				

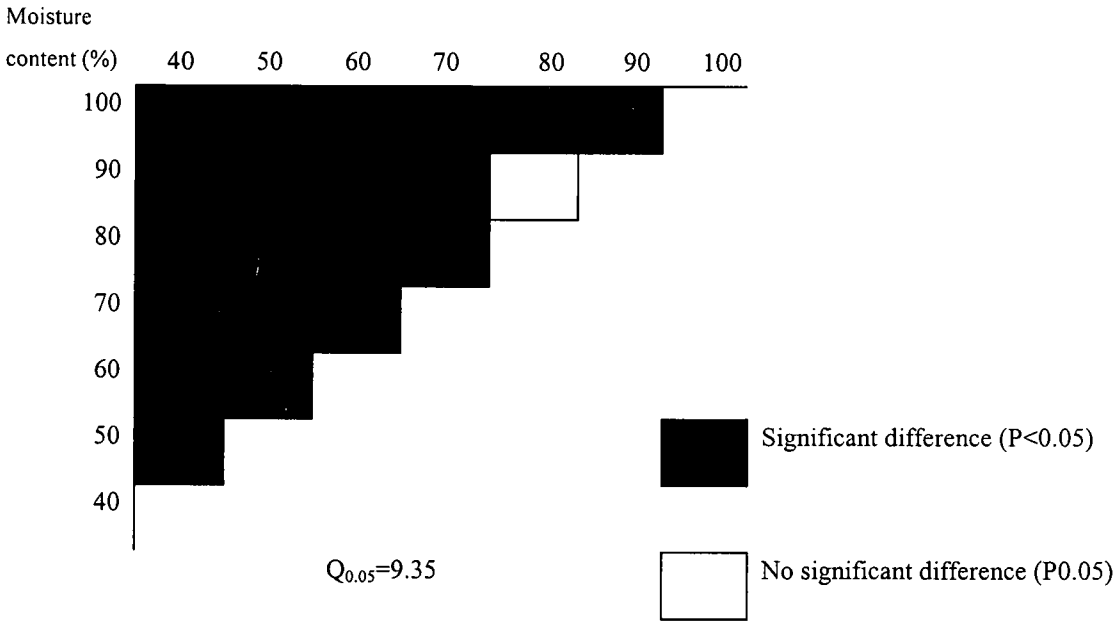


Figure A4.12: A schematic presentation of the significant differences in survival of *Coproica hirtula* pupae at different moisture content.

Table A4.13: Analysis of variance of the total immature development of *Coproica vagans* at different moisture content.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	10844.3922	6	1807.3987	21.3754992	1.6237E-13	2.24640928
Error	5326.94545	98	84.5546897			
Total	16171.3377	104				

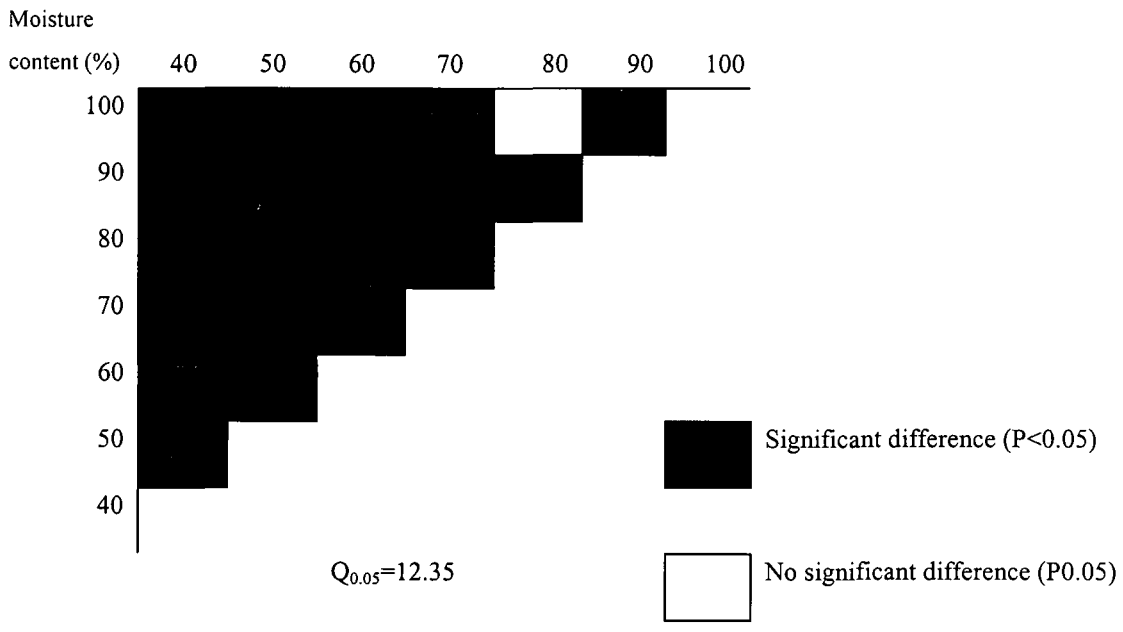


Figure A4.13: A schematic presentation of the significant differences in the number of *Coproica vagans* eggs reaching adulthood at different moisture content.

Table A4.14: Analysis of variance of the total immature development of *Coproica hirtula* at different moisture content.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	13269.322	6	2211.55367	62.3163662	4.0035E-26	2.23118946
Error	2484.23916	98	35.4891309			
Total	15753.5612	104				

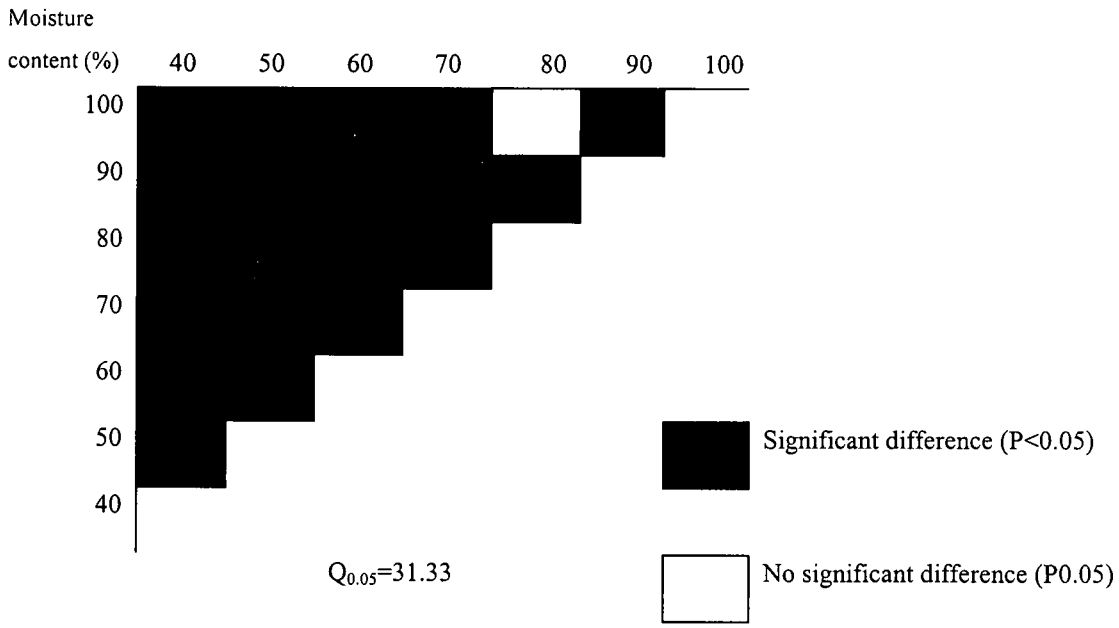


Figure A4.14: A schematic presentation of the significant differences in the number of *Coproica hirtula* eggs reaching adulthood at different moisture content.

Table A4.15: Analysis of variance of the life expectancy of *Coproica vagans* adults at different moisture content.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	1021.74286	6	170.290476	19.4142237	1.1276E-12	2.24640928
Error	552.6	63	8.77142857			
Total	1574.34286	69				

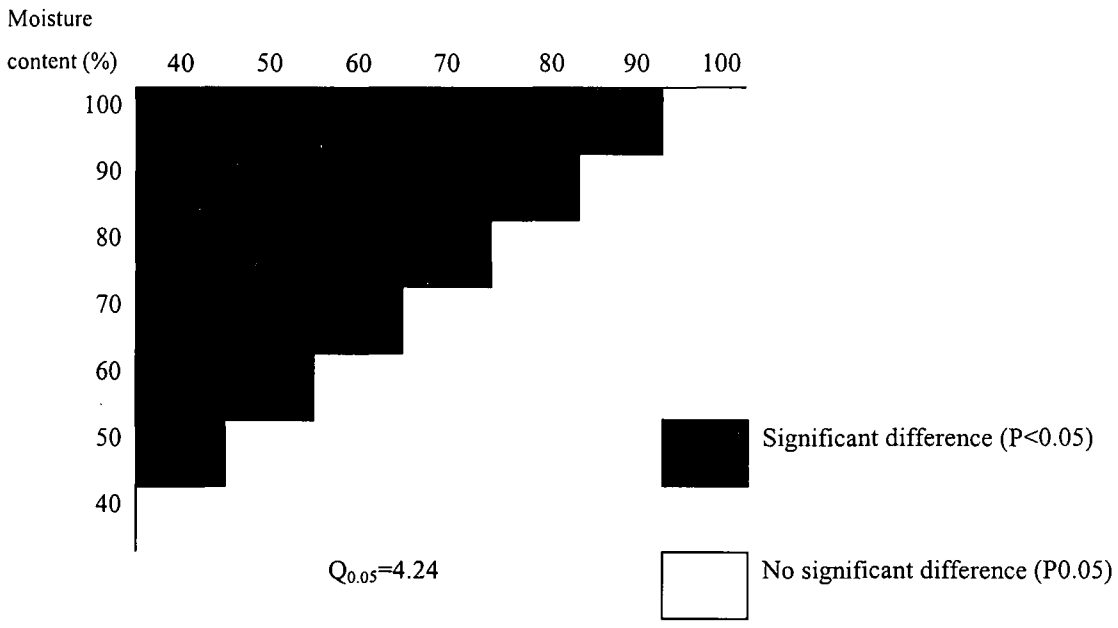


Figure A4.15: A schematic presentation of the significant differences in the life expectancy of *Coproica vagans* adults at different moisture content.

Table A4.16: Analysis of variance of the life expectancy of *Coproica hirtula* adults at different moisture content.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	1769.42857	6	294.904762	64.9161426	1.21E-26	2.23118946
Error	318	63	4.54285714			
Total	2087.42857	69				

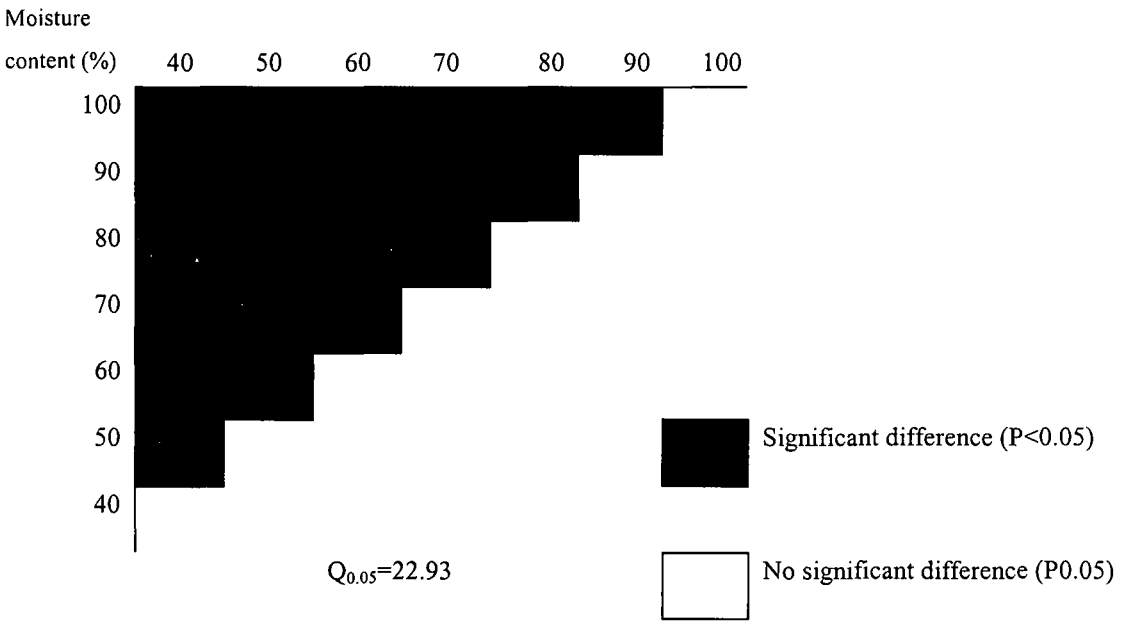


Figure A4.16: A schematic presentation of the significant differences in the life expectancy of *Coproica hirtula* adults at different moisture content.

Table A 4.17: Results from t-tests (indicated by P-values) in comparing development times between *Coproica vagans* and *Coproica hirtula* of all stages at different moisture content.

Moisture content (%)	40	50	60	70	80	90	100
Eggs	0.048*	0.025*	0.029*	0.030*	0.038*	0.040*	0.041*
Larvae	0.033*	0.999	0.999	0.038*	0.999	0.202	0.047*
Pupae	0.999	0.030*	0.701	0.999	0.029*	0.015*	0.042*

(* indicate significant difference [P<0.05])

Table A 4.18: Results from t-tests (indicated by P-values) in comparing survival rates between *Coproica vagans* and *Coproica hirtula* of all stages at different moisture content.

Moisture content (%)	40	50	60	70	80	90	100
Eggs	0.002*	0.010*	0.012*	0.033*	0.034*	0.049*	0.035*
Larvae	0.045*	0.011*	0.041*	0.031*	0.029*	0.028*	0.033*
Pupae	0.018*	0.022*	0.039*	0.010*	0.040*	0.035*	0.013*
% Eggs reaching adulthood	0.090	0.043*	0.021*	0.030*	0.032*	0.019*	0.047*

(* indicate significant difference [P<0.05])

CHAPTER 5

THE EFFECT OF CONSTANT TEMPERATURE AND PHOTOPERIOD ON THE OVIPOSITION OF *COPROICA VAGANS* AND *COPROICA HIRTULA*

5.1 INTRODUCTION

Various authors have studied the oviposition behaviour of several Diptera species under laboratory conditions. Porchinsky (1885) was among the first to examine the fauna of cow droppings in Russia, while Bay *et al.* (1969) investigated the oviposition and development of the face fly, *M. autumnalis,* in faeces of different animals in the USA. Oviposition studies by Hower & Cheng (1968), also in the USA, have shown that face flies lay their eggs in several batches in cow manure. Recently Lachmann (1991) studied the egg development of two species, *C. lugubris* and *C. scutellaris* (Sphaeroceridae), although more attention was given to mating behaviour than oviposition. Hammer (1941) and Teskey (1960) dissected *M. autumnalis* to determine the number of eggs present in the ovaries and found as many as 31 eggs per female. Hammer (1941) also dissected several Sphaeroceridae species, including *Sphaerocera*, *Chaetopodella* and *Pullimosina* species, and found between 16 and 32 eggs per pair of ovaries.

Since nothing could be found in the literature regarding the oviposition behaviour of *C. vagans* or *C. hirtula*, the current study on egg production of the two species was undertaken. In developing any effective physical method to control the Sphaeroceridae, knowledge on the total number of eggs oviposited by a female during her lifetime, as well as frequency of egg deposition, is essential. This issue was approached in two ways:

(1) What is the influence of constant temperature on ovipostion and frequency of egg deposition? This knowledge is essential to determine whether extreme temperatures had any influence on egg production and if it does, to what degree;

(2) What is the effect of photoperiod on the oviposition behaviour of *C. vagans* and *C. hirtula*?

5.2 MATERIAL AND METHODS

Sterilized cattle dung (100 % moisture content) was placed into Apex vials No.8 (75 x 25 mm) to a depth of approximately one centimetre (see 4.2.1) and leveled to facilitate the counting of the eggs. Any cracks or little holes present in the dung, resulted in the majority of eggs being deposited in these depressions, making the counting of the eggs more difficult. Two-day-old *C. vagans* and *C. hirtula* females from a laboratory colony (F2) were used in this experiment. Flies were collected with an aspirator and anaesthetized with CO^2 to separate the sexes. The females were individually transferred to the vials. Eggs were deposited in batches and any eggs deposited on the glass sides of the Apex vials were removed, as they tended to dry out. Fortunately the females never oviposited inside the dung, but simply deposited the eggs on the surface of the dung, which made counting much easier.

5.2.1 Influence of various constant temperatures

This experiment was conducted in incubators set at various constant temperatures ranging from 12°C to 36°C with 6°C intervals. Since it was found that the adult flies did not survive at 6°C or 42°C, (see Fig. 4.10), oviposition behaviour was not studied at these temperatures. Prior to the onset of the experiment, the vials with dung were preconditioned to the various experimental temperatures and were closed with perforated stoppers to allow ventilation. A day:night cycle of 12 hours light and 12 hours dark was maintained. In each treatment 10 replicates were used and the experiment was repeated three times. Observations were made every 24 hours and the number of eggs produced was counted. To determine the oviposition period and total number of eggs produced per day, this procedure was followed until all the female flies had died. The pre-oviposition

period, *i.e.* the period from fly emergence until the first eggs were produced, was also determined at the different temperatures.

5.2.2 Influence of different photoperiods

Egg production by females exposed to various photoperiods was conducted in incubators set at 24°C ± 1°C with various light regimes. The following photoperiods were used: light:dark cycle of 24:0, 18:6, 12:12, 6:18 and 0:24 hours. The same experimental procedure in preparing the vials was followed as described in 5.2.1. Before the onset of the experiment, the vials were preconditioned at 24°C. There were 10 females for each photoperiod and the experiment was repeated three times. Observations were made every day and the number of eggs was counted. The oviposition period, which included the time from emergence until all the female flies had died, was also determined. At the light:dark cycle of 0:24 hours, females were briefly exposed to a very dim light when they were transferred to newly prepared vials every day and immediately placed back into the dark again. In this case the number of eggs produced during each 24 hour-period was also counted and documented.

5.3 RESULTS AND DISCUSSION

5.3.1 The influence of temperature on ovipostion

The pre-oviposition period, *i.e.* the period from fly emergence until the first eggs were laid, was also affected by temperature. At cooler temperatures such as 12°C, the pre-oviposition periods were longer for both species, while at the higher temperatures, such as 30°C and 36°C, this period was 2.0 ± 0.1 and 2.0 ± 0.15 days respectively. It is also important to note that the pre-oviposition period was the same for both species at each of the different temperatures (Fig. 5.1).

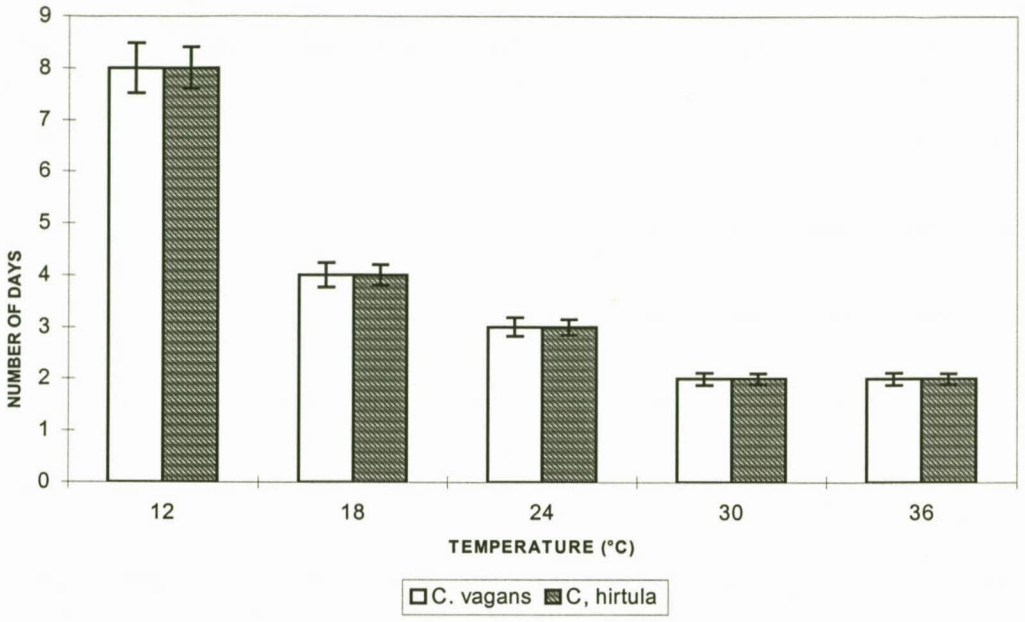


Figure 5.1: The pre-oviposition period of *Coproica vagans* and *Coproica hirtula* at different constant temperatures.

The oviposition period for both species showed the same trend as temperature increased. At 36°C, the females of *C. vagans* and *C. hirtula* oviposited over a period of 7.5 ± 0.6 and 7.0 ± 0.65 days respectively (Fig. 5.2). Although the life span of adults was much longer at 12°C than at 18°C, it is important to note that the oviposition period was shorter at 12°C than at 18°C for both species. At 18°C oviposition by *C. hirtula* took place for 21 ± 2.1 days (Fig. 5.2).

With analysis of variance ($F_{45;4}$=21.59) significant differences ($P<0.05$) were shown in oviposition duration for *C. vagans* (Table A5.1). Tukey's test ($Q_{0.05}$=13.66) showed that the duration of oviposition at 18°C and 24°C differed significantly from each other and also from those at the other temperatures regimes, but no significant differences were shown between 30°C and 36°C (Fig. A5.1). For *C. hirtula*, analysis of variance ($F_{45;4}$=21.27) also showed significant differences ($P<0.05$) in the duration of oviposition (Table A5.2). Tukey's test ($Q_{0.05}$=12.58) again indicated that these significant differences were between duration of oviposition at 18°C, 24°C and all other temperatures but not

between 30°C and 36°C (Fig. A5.2). A t-test was also conducted in which the mean of two samples was compared. The duration of oviposition between *C. vagans* and *C. hirtula* differed significantly ($P<0.05$) at 18°C to 30°C, but no significant differences ($P>0.05$) existed between the two species at 12°C or 36°C (Table A5.7).

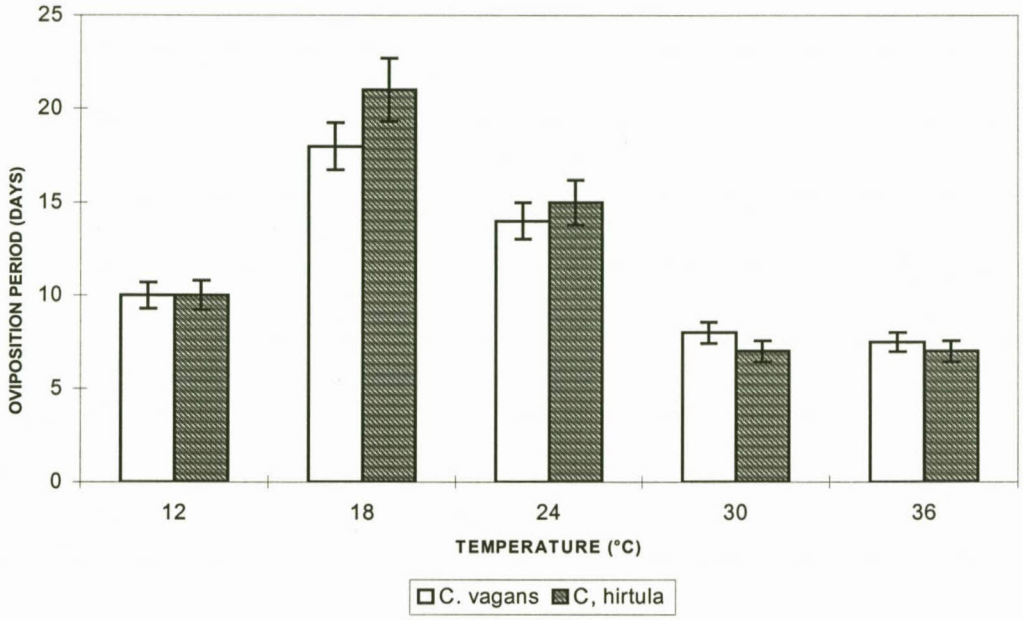


Figure 5.2: The duration of oviposition by *Coproica vagans* and *Coproica hirtula* at different constant temperatures.

Oviposition studies at different constant temperatures revealed that temperature exerted strong effects on all reproductive parameters of Sphaeroceridae that were investigated. Firstly the effect of temperature on pre-oviposition periods and duration of ovipostition showed a noticeable trend, in which pre-oviposition periods and duration of oviposition increased with a decrease in temperature. This is in agreement with findings by Larsen & Thomsen (1940) who showed that *Sarcophaga stimulans* Walker (Sarcophagidae) had a pre-ovipositional period of about 25 days at 15°C and 14 days at 20°C. According to literature references, many other oviposition studies were conducted which involved different Sphaeroceridae species. Goddard (1938) for example found that *P. heteroneura*

females started ovipositing five to 12 days after copulation and continued for a period of up to 32 days at 25°C, although pre-oviposition periods for *C. vagans* and *C. hirtula* were much shorter. In the case of *S. parapusio,* oviposition began on the fifth day after emergence and the eggs were laid over a period of five days at ambient temperatures (Okely, 1974). He also found that the females of *P. pullala* (Zetterstedt) (Sphaeroceridae) commence ovipositing on the fourth day after emergence and lay up to 80 eggs during a 20 day period at about 20°C to 25°C (Okely, 1974). As far as other fly species are concerned, Wang (1964) found that at 25°C to 30°C, and 50% to 70% relative humidity, as well as on a special diet of sugar, milk and blood, face flies started mating four to five days after emergence and started ovipositing two to five days after the first mating. They continued ovipositing throughout their life span which ranged from three weeks up to three months (Wang, 1964). Results from the current study showed that although the life span of *C. vagans* and *C. hirtula* was much shorter, but they also continued to oviposit for the duration of their life span. However, a decrease in oviposition was noticed towards the end of the adult life span.

The average total number of eggs produced by individual *C. vagans* and *C. hirtula* females were 607 ± 71 and 544 ± 65 respectively (Fig. 5.3). In both cases, these eggs were oviposited at 24°C, while at temperatures above and below 24°C, the total number of eggs produced was lower (Fig. 5.3). At the highest experimental temperature (36°C), females of both species produced more eggs than at 12°C, the lowest experimental temperature. At 12°C, individual *C. vagans* and *C. hirtula* females produced a total of only 8.0 ± 0.01 and 5.0 ± 0.01 eggs respectively (Fig. 5.3). No egg production occurred below 12°C or above 36°C, because the adult flies did not survive for longer than one day at these extreme temperatures. *Coproica vagans* also produced significantly more eggs at all the different temperatures than *C. hirtula* (Fig. 5.3).

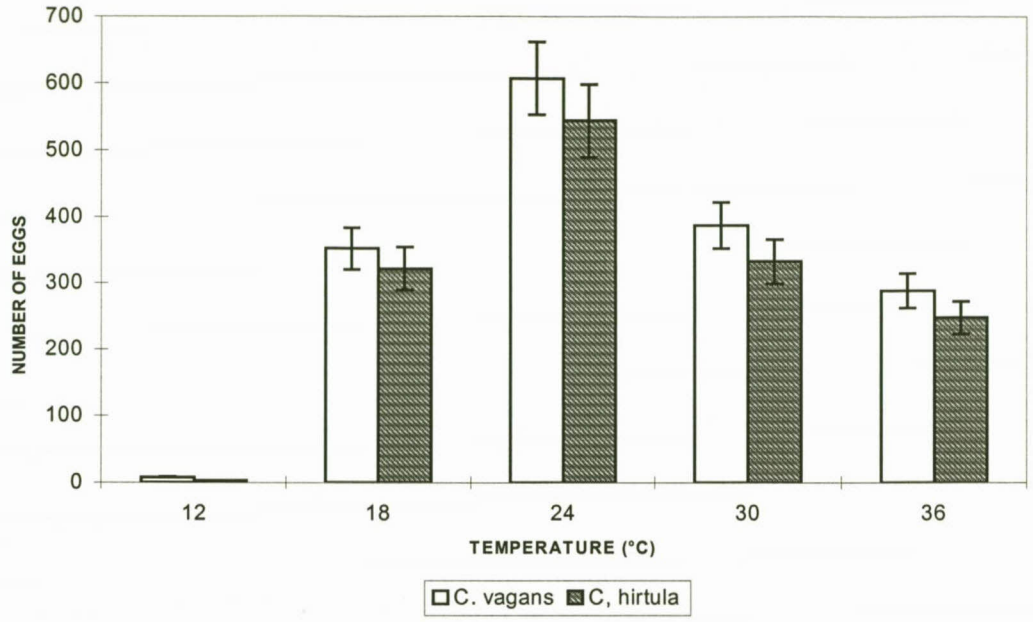


Figure 5.3: The total number of eggs oviposited by *Coproica vagans* and *Coproica hirtula* females at different constant temperatures.

Analysis of variance ($F_{70;4}$=25.17) showed that significant differences ($P<0.05$) existed in the total number of eggs produced by *C. vagans* females at different constant temperatures (Table A5.3). Tukey's test ($Q_{0.05}$=16.67) showed that the total number of eggs oviposited at 24°C was significantly more than those oviposited at the other temperatures. The number of eggs produced at 12°C was also significantly less than those produced at the other temperatures in the range (Fig. A5.3). As far as *C. hirtula* is concerned, the analysis of variance ($F_{70;4}$=23.60) indicated that significant differences ($P<0.05$) existed in the total number of eggs produced by this species at the different temperatures (Table A5.4). Tukey's test ($Q_{0.05}$=11.31) showed that significant differences also existed between the total number of eggs produced at 12°C and 24°C. The total number of eggs produced at 12°C and 24°C also differed significantly from the rest of the experimental temperatures (Fig. A5.4). To compare the total number of eggs produced by *C. vagans* and *C. hirtula* females with each other, a statistical t-test was used. Significant differences ($P<0.05$) between the two species were shown at all the

various temperatures where oviposition was monitored, except at 12°C, where no significant differences (P>0.05) existed (Table A5.7).

A comparison between the mean number of eggs produced per day by *C. vagans* and *C. hirtula* females are shown in Table 5.1. These results clearly showed that at 12°C, very few eggs were laid (average of 0.06 - 0.3), even though the female flies survived for up to 66 days at 12°C (see Chapter 3). At the higher temperatures on the other hand, egg production commenced on the first day and all the eggs were oviposited in the first 7 to 10 days (Fig. 5.2). The mean number of eggs produced per day was also higher at 30°C and 36°C compared to the lower temperatures (Table 5.1).

Table 5.1. The average number of eggs laid per day for *Coproica vagans* and *Coproica hirtula* at different constant temperatures.

Temperature	*Coproica vagans*	*Coproica hirtula*
12°C	0.30	0.06
18°C	10.6	8.00
24°C	24.8	22.7
30°C	33.3	28.7
36°C	24.9	28.5

In the vials the eggs of both *C. vagans* and *C. hirtula* were randomly scattered on the surface of the dung. Even though attempts were made to prevent the formation of depressions in the dung, very fine cracks or holes were sometimes still present, and most of the eggs were then deposited in these depressions. Hammer (1941) maintained that depositing eggs in depressions or cracks in dung may be of ecological significance, because these eggs would be protected against desiccation and predation and therefore the risk of perishing becomes less. He found that certain species such as *Spelobia clunipes* (Meigen) (Sphaeroceridae) and *C. scutellaris* females lay eggs in small holes in

cow pats in Denmark and cover it with their own excrement. In Britain it was found that the eggs of *Limosina silvatica* (Meigen) (Sphaeroceridae) were buried in decaying grass (Goddard, 1938). No such behaviour was observed in *C. vagans* or *C. hirtula* adults. Wang (1964) also stated that in dry dung, face flies deposited eggs in cracks, small pits and depressions where the accumulated moisture delayed drying and hardening of the dung, while on fresh dung, eggs were deposited randomly over the surface, sometimes individually or in batches of five to eight eggs. The Australian bush fly *M. vetustissima* laid their eggs under the rim of dung pats near the interface between the faecal material and the substrate on which it was dropped (Greenham, 1971).

Within the limits of the temperature range that permits reproduction, oviposition has been shown to be extremely temperature sensitive in both Sphaeroceridae species. The relationship between temperature and oviposition indicated that egg production is maximal at temperatures fairly close to the upper limit of development and survival of eggs, decreasing steeply at lower temperatures and more gradually at higher temperatures (Fig. 5.3). In both species maximum oviposition rates were obtained at 24°C, which confirmed that 24°C might be the optimal temperature for maintaining laboratory colonies of Sphaeroceridae. Very few eggs were laid when females were maintained at a constant temperature of 12°C. This temperature was probably close to the lower threshold temperature for oviposition. These findings are in accordance with those of Lee & Denlinger (1985b) who found that reproduction was adversely affected by extremes of temperatures, more readily than most other physiological functions. The range of temperatures over which reproduction will occur is correspondingly limited. The exact nature and extent of the temperature range varies from species to species and either sex may suffer ill effects. *Anopheles quadrimaculatus* Say (Culicidae) females, for instance, will also not lay eggs if the temperature drops below 12°C (Mayne, 1926).

Another way in which higher temperatures may affect reproduction was shown by Young & Plough (1926), where they found that when *Drosophila subobscura* Collin was kept at 32°C, a proportion of the males were rendered permanently sterile. Similarly exposure to 34°C for more than 24 hours also had a sterilizing effect on males of *M. domestica* (Michelsen, 1960). This demonstrates the rather critical nature of reproduction when compared to other physiological functions, which can be sustained over a wider range of temperatures (Mayne, 1926).

Hammer (1941) was among the first to report extensively on oviposition habits of flies. Several Sphaeroceridae species were dissected by Hammer (1941) to determine the number of eggs present in both the ovaries. These results are summarized in Table 5.2.

Table 5.2. Total number of eggs present in dissected ovaries of Sphaeroceridae species, according to Hammer (1941).

Species	Average number of eggs N=150
Lotobia pallidiventris (Meigen)	20.0
Ischiolepta pusilla (Fallèn)	29.0
Sphaerocera subsultans Linnaeus	19.7
Spelobia crassimana (Haliday)	29.0
Chatopodella scutellaris (Haliday)	20.6
Pullimosina moestra (Villeneuve)	16.5
Lotophila atra (Meigen)	25.0
Borborillus sordidus (Zetterstedt)	32.0

Although oviposition patterns of *C. vagans* and *C. hirtula* were different from other examples of Sphaeroceridae in the literature, a brief summary of these literature findings is presented for the purpose of comparing the results. Among other Sphaeroceridae,

Fredeen & Taylor (1964) showed that *L. caenosa* females in Canada might produce only 10 eggs per day during their early life. However, they are long-lived (up to 79 days) and are capable of producing more than 1000 eggs in total. The last fertile eggs were laid 47 days after fertilization (Fredeen & Taylor, 1964). Goddard (1938) found that a single *P. heteroneura* female oviposited about 60 to 70 eggs, scattered on the surface of the rearing medium. The females of the fungivorous *S. parapusio* produced a large number of eggs (40 - 100) in regular lines along the fills of the mushroom cap (Okely, 1974). Among other fly species, Killough & McClellan (1965) found that face flies (*M. autumnalis*) deposited eggs in batches of about 20 per batch, with two to eight days between batches and they kept this egg production rates during their entire life span. One female was reported to have produced 220 eggs in 58 days (Killough & McClellan 1965).

The fact that the daily rate of oviposition is maximal at a given temperature does not mean that this will be the temperature at which the greatest number of eggs will be produced. Although previous results showed that for both *C. vagans* and *C. hirtula* the optimum temperature for development and survival was 24°C, this was also the temperature at which most of the eggs were produced. However, this does not agree with the findings of Graham *et al.* (1967), who maintained that oviposition of flies usually happens in such a way that total egg production is maximal at a temperature slightly lower than the optimum temperature for development and survival of eggs.

Although oviposition was not determined at feedlot conditions, temperature will undoubtedly also has an effect on oviposition in the field. Mohr (1943) found that if the evenings cooled down too much, oviposition by face flies (*M. autumnalis*) did not take place at all. Hammer (1941) found that *M. tempestiva* in Denmark oviposited only a few times, mainly on droppings with a distinct crust and a surface temperature of 24°C. Although oviposition sites of mosquitoes differ from those of dung breeding flies, Oda *et*

al. (1980) found that *Culex pipiens* Linnaeus (Culicidae) laid eggs at 21°C to 28°C, but that the rate of oviposition decreased markedly at temperatures above 30°C.

There was no definite pattern in which oviposition took place. At 24°C for example, oviposition only started on the third day after both species were introduced to the vials. Some females deposited large numbers of eggs, whilst others oviposited only a few, sometimes as low as one egg per day. Some females oviposited only for one or two days during their life span, while others produced eggs for as long as 15 consecutive days. However, there was a tendency to produce a large number of eggs on one day, followed by a smaller number or no eggs the following day. This was however, not a hard and fast rule, because numerous females produced large numbers of eggs for two or three consecutive days before the oviposition rate declined. Some females only increased their oviposition rate later on in their life. Some *C. vagans* females, for instance, produced eggs regularly for 18 days, while at lower temperatures, eggs were still produced on day 21. The decrease in egg production over time could also be attributed to the age of the females. Among other fly species, Wang (1964) reported that, depending on temperature, photoperiod and diet, the number of eggs per female face fly in the USA ranged from 30 to 128 and are oviposited in batches of 6 to 26, at intervals of several days. Bay *et al.* (1969) also studied the oviposition behaviour of the face fly, *M. autumnalis*, and found that each female laid an average of 143 eggs in fresh dung over a period of 10 to 15 days. As far as other Diptera species such as mosquitoes are concerned, Herms & Freeborn (1920) found that 33 females of *Anopheles punctipennis* (Say) oviposited 33 times, with batches ranging from 83 to 321 eggs each with a total of 6700 eggs. On average, 203 eggs per oviposition were produced. Twenty-nine females of *An. quadrimaculatus* oviposited 30 times, in batches ranging from 140 to 315 eggs, totaling 6282 eggs. The average number of eggs per oviposition was 209 eggs (Herms & Freeborn, 1920).

A doubt must remain whether data obtained under constant temperature laboratory conditions can support rigid application to populations of flies in a natural environment. There is evidence, for instance, that a few days of exposure to low temperature may cause considerable augmentation of the rate of oviposition. Maynard-Smith (1958) have shown that exposure to 30.5°C during the early adult life of *D. subobscura* greatly reduced the rate of oviposition during later life. Effects of this kind suggested that, with fluctuating temperatures that characterize natural habitats, egg production might not bear any simple relationship to mean temperature. Hower & Cheng (1968) also made it clear that oviposition behaviour of flies held in captivity might be different from those living under natural conditions. However, despite such complications of detail, it is probably safe to assume that an increase in environmental temperature between 0°C and 25°C will cause a marked increase in the rate of reproduction of most fly populations and in this way exert an effect on population density.

5.3.2 The influence of photoperiod on oviposition

A day-night cycle of 12 hours light and 12 hours dark seemed to be the preferred photoperiod for oviposition under experimental conditions for both *C. vagans* and *C. hirtula*. An avergage total of 598 ± 69 eggs and 565 ± 67 eggs were oviposited for *C. vagans* and *C. hirtula* respectively. The other four light-dark regimes resulted in the oviposition of fewer eggs by the females (Fig. 5.4). The mean number of eggs produced per female on a daily basis for both *C. vagans* and *C. hirtula* is shown in Table 5.3. These results also indicated that the 12L:12D-cycle was the best photoperiod in terms of the number of eggs produced per day. However, the lowest mean number of eggs was produced by the females of both species at (6L:18D) regime. At 18L:6D and 12L:12D-cycles, *C. vagans* females produced significantly more eggs on average than *C. hirtula*, while at the darker intervals (6L:18D and 0L:24D), oviposition by *C. hirtula* was significantly higher (Table 5.3).

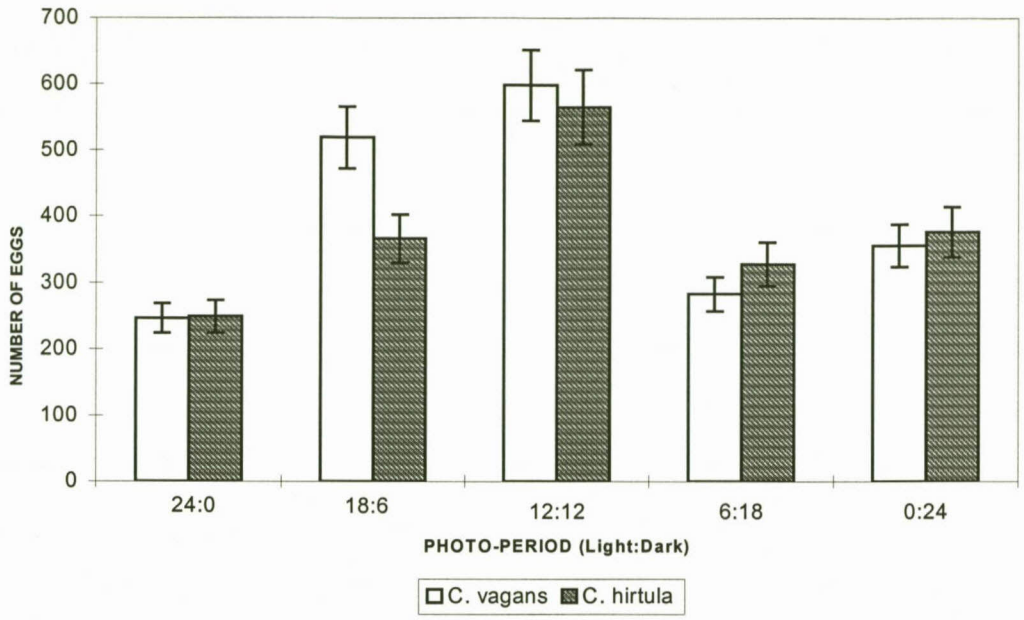


Figure 5.4: The total number of eggs laid per female by *Coproica vagans* and *Coproica hirtula* at different photoperiods.

Table 5.3. The average number of eggs laid per female per day for *Coproica vagans* and *Coproica hirtula* at different photoperiods.

Photoperiod	*Coproica vagans*	*Coproica hirtula*
24L:0D	15.4	15.8
18L:6D	22.1	15.6
12L:12D	24.8	22.7
6L:12D	10.2	11.5
0L:24D	12.5	16.4

With analysis of variance ($F_{55;4}$=5.45), significant differences (P<0.05) were shown to exist in the total number of eggs produced at different photoperiods by *C. vagans* females (Table A5.5). Tukey's test ($Q_{0.05}$=2.38) showed that the total number of eggs oviposited at 12L:12D and 18L:6D-intervals differed significantly from each other and also from those tested at the other photoperiods (Fig. A5.5). The total number of eggs

oviposited at 24L:0D was significantly lower compared to the rest of the photoperiods (Fig. A5.5). For *C. hirtula*, an analysis of variance ($F_{5;5;4}$=5.98) also showed significant differences ($P<0.05$) in the total number of eggs produced by the females at the different photoperiods (Table A5.6). Tukey's test ($Q_{0.05}$=11.31) indicated that the maximum number of eggs produced at 12L:12D-cycle differed significantly from the values at the other photoperiods, while the number of eggs produced at 24L:0D was significantly lower compared to the other photoperiods (Fig. A5.6). However, no significant differences were found between 18L:6D and 0L:24D photoperiods (Fig. A5.6). In conducting a t-test, significant differences ($P<0.05$) in the total number of eggs oviposited between *C. vagans* and *C. hirtula* were shown at all the various photoperiods which were monitored. The only exception was the complete dark interval (0L:24D) where no significant difference ($P>0.05$) in numbers occurred between the two species (Table A5.8).

In an overview of oviposition at different photoperiods, it became evident that oviposition took place at all photoperiods regardless of the duration of any light or dark cycle. Although oviposition was higher at some photoperiods than others, results showed that oviposition continued even in the absence of light. Flies that were kept in darkness all the time (0L:24D) were exposed to light for only a few seconds every day when they were transferred to freshly prepared vials. It could be that this short light exposure provided enough stimuli to encourage egg production in the two sphaerocerid species. None the less, both Sphaeroceridae species deposited eggs freely on the dung in constant darkness (0L:24D), indicating that light was not essential for egg deposition. One possible explanation for this was given by Corbett (1963) who suggested that such behaviour in constant darkness provides enough evidence that certain flies lack an endogenous photoperiodicity and is therefore not truly circadian in its usual sense. This could also be the case for these two Sphaeroceridae. Fredeen & Glen (1970) also found that in the case of *L. caenosa*, mating, feeding and ovipositing took place within the confines of the rearing containers even in complete darkness. The reason for the poor

performance in oviposition by both species at the 6L:18D interval is difficult to explain, since more eggs were produced in total darkness (0L:24D) than at 6L:18D. It could be that the six hours of light was just at a critical minimum level and that egg production was not stimulated effectively. However, these results could also implicate that flies will mainly oviposit at the feedlot during the day and that oviposition might drop during the night. Observations at the feedlot during summer also showed that fly activity was low at night, which then allowed the cattle to feed, whereas they avoided the feeding troughs during the day when fly activity was exceptionally high. Mohr (1943), in studies on the succession of flies in the USA, also found that the degree of light on droppings in the open pastures did have a noticeable effect on oviposition, because some of the early succession species failed to oviposit in dung dropped earlier at night. Parrella (1984) furthermore indicated that the onset of photophase triggered the ovipositional response of *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae) and, as was also demonstrated in this study, different temperatures modified this response. Blanckenhorn (1998) investigated the diapause response in two geographically and altitudinally widespread dung flies *Scathophaga stercoraria* (Linnaeus) (Diptera: Scathophagidae) and *Sepsis cynipsea* (Linnaeus) (Diptera: Sepsidae), and maintained that temperature had more influence on both species than photoperiod, also with regards to their fecundity. The decrease in Sphaeroceridae egg production at the feedlot during winter could therefore also be influenced by the duration of the photophase, and not only by the lower nocturnal winter temperatures.

Oviposition by both species at a total light regime (24L:0D) resulted in the lowest egg production rates recorded, which was even lower than in darkness. This does not agree with the findings of Wang (1964) who showed in studies with face flies that longer hours of light resulted in more eggs per female. For instance, 30-35 eggs/female at eight hours of light, 60-80 eggs at 16 hours light and 128 eggs at 24 hours light (Wang, 1964). He contributed this to the fact that feeding is an important factor in determining the rate of development and reproductive potential of flies (Wang, 1964). Under a short daily

photoperiod, Wang (1964) maintained that because adults fed less, reproductive activity was lowered. It seemed on the other hand as if Sphaeroceridae flies needed a day-night rhythm in which the day and night cycles were equal in length. This is in agreement with the findings of Logen & Harwood (1965), who found that oviposition by *Culex tarsalis* Coquillett (Culicidae) displayed a bimodal pattern, in which egg laying occurred during the first few hours of the photo-phase, but that oviposition was largely suppressed under continuous light. Gillett *et al.* (1959) also noted that for *Aedes aegypti* (Linnaeus) (Culicidae), alternating light and dark were necessary for an oviposition rhythm to occur. Other laboratory studies were done by Flitters (1964) on the reproduction behaviour of the Mexican fruit fly, *Anastrepha ludens* (Loew) (Diptera: Tephritidae). Although this species differs considerably from Sphaeroceridae in terms of feeding behaviour and oviposition sites, Flitters (1964) was able to demonstrate that oviposition occurred principally during the late photo-phase and that the ovipositional rhythm also continued under conditions of continuous darkness if the temperature remained constant. This indicates a similarity between the Sphaeroceridae and this particular Tephritidae species as far as their oviposition behaviour in continuous darkness is concerned. Further investigations by Pittendrich & Bruce (1959) into the photoperiodically entrained endogenous rhythm of flies showed that oviposition was also dependent on the physiology of the ovarian cycle of flies, which was sensitive to temperature but not to photoperiod. They found that although the oviposition rhythm is photoperiodically regulated, the ovarian cycle was found to determine whether or not oviposition would occur on a given day (Pittendrich & Bruce, 1959).

Further studies on this subject should be pursued to obtain an accurate knowledge of egg distribution especially because egg density might be used as an index of Sphaeroceridae populations in an area. Also, a clear understanding of oviposition habits of Sphaeroceridae under natural conditions will greatly assist research pertaining to its control.

5.4 APPENDIX

Table A5.1: Analysis of variance of the duration of oviposition by *Coproica vagans* adult flies at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	5968.12	4	1492.03	21.5895527	5.3757E-10	2.57873722
Error	3109.9	45	69.1088889			
Total	9078.02	49				

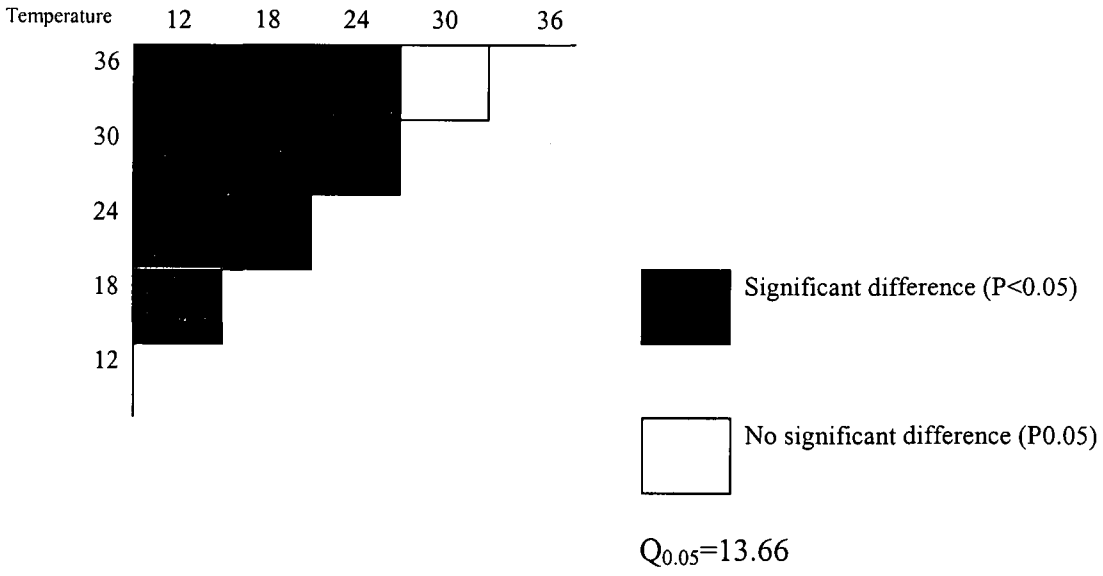


Figure A5.1: A schematic presentation of the significant differences in duration of oviposition of *Coproica vagans* at different constant temperatures.

Table A5.2: Analysis of variance of the duration of oviposition by *Coproica hirtula* adult flies at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	7146.88	4	1786.72	21.265413	6.6872E-10	2.57873722
Error	3780.9	45	84.02			
Total	10927.78	49				

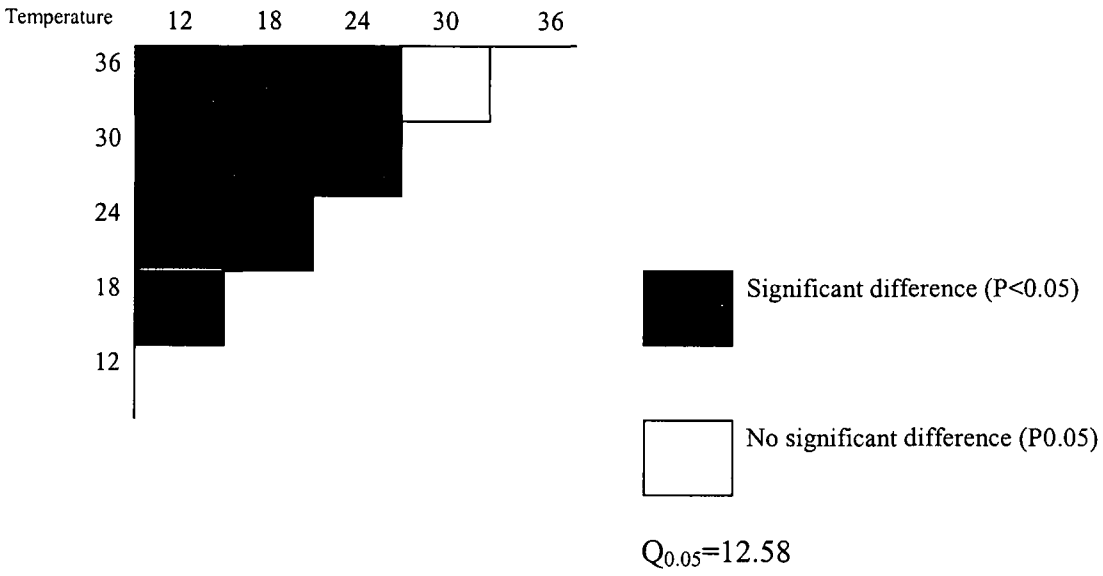


Figure A5.2: A schematic presentation of the significant differences in duration of oviposition of *Coproica hirtula* at different constant temperatures.

Table A5.3: Analysis of variance of the total number of eggs produced by *Coproica vagans* adults at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	689379	4	172344.75	25.1688399	5.4939E-11	2.57873722
Error	308139.5	70	6847.54444			
Total	997518.5	74				

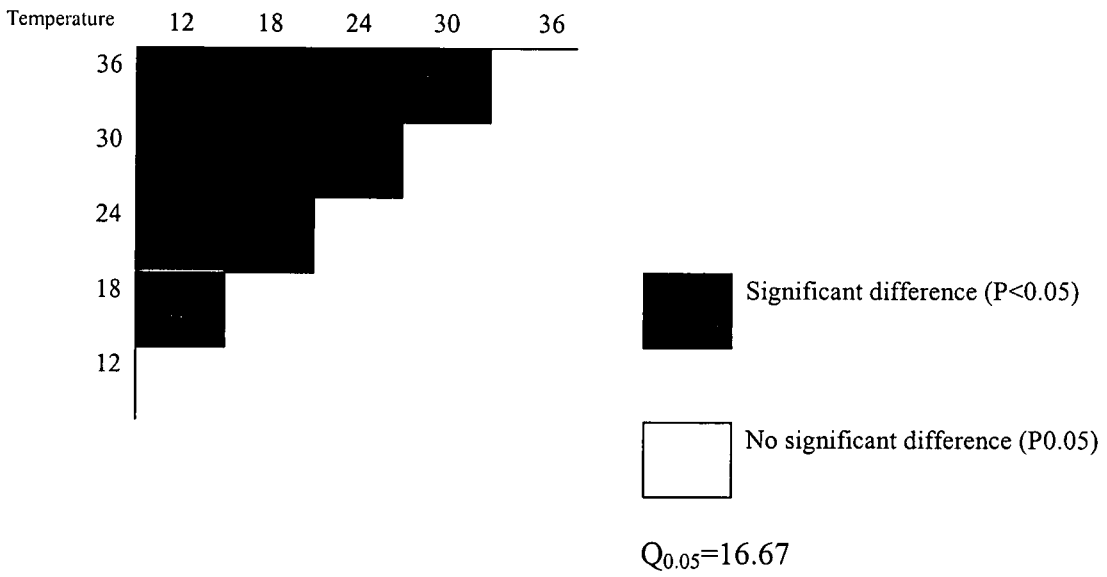


Figure A5.3: A schematic presentation of the significant differences in the total number of eggs oviposited by *Coproica vagans* at different constant temperatures.

Table A5.4: Analysis of variance of the total number of eggs produced by *Coproica hirtula* adults at different constant temperatures.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	482535.72	4	120633.93	23.5963916	1.455E-10	2.57873722
Error	230057.5	70	5112.38889			
Total	712593.22	74				

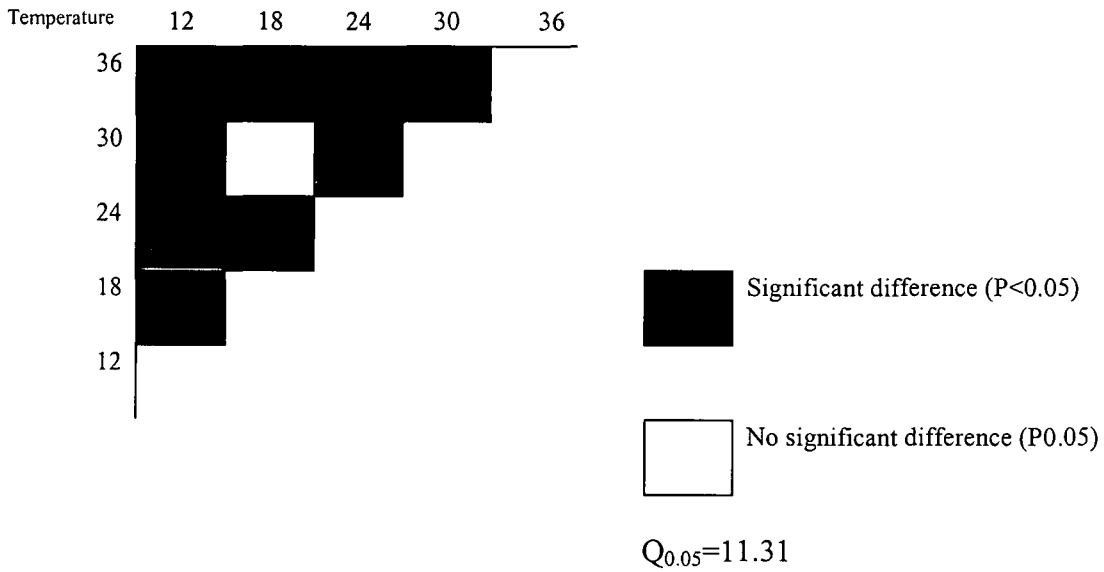


Figure A5.4: A schematic presentation of the significant differences in the total number of eggs oviposited by *Coproica hirtula* at different constant temperatures.

Table A5.5: Analysis of variance of the total number of eggs produced by *Coproica vagans* adults at different photoperiods.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	212130.48	4	53032.62	5.44912291	0.00115238	2.57873722
Error	437954.5	55	9732.32222			
Total	650084.98	59				

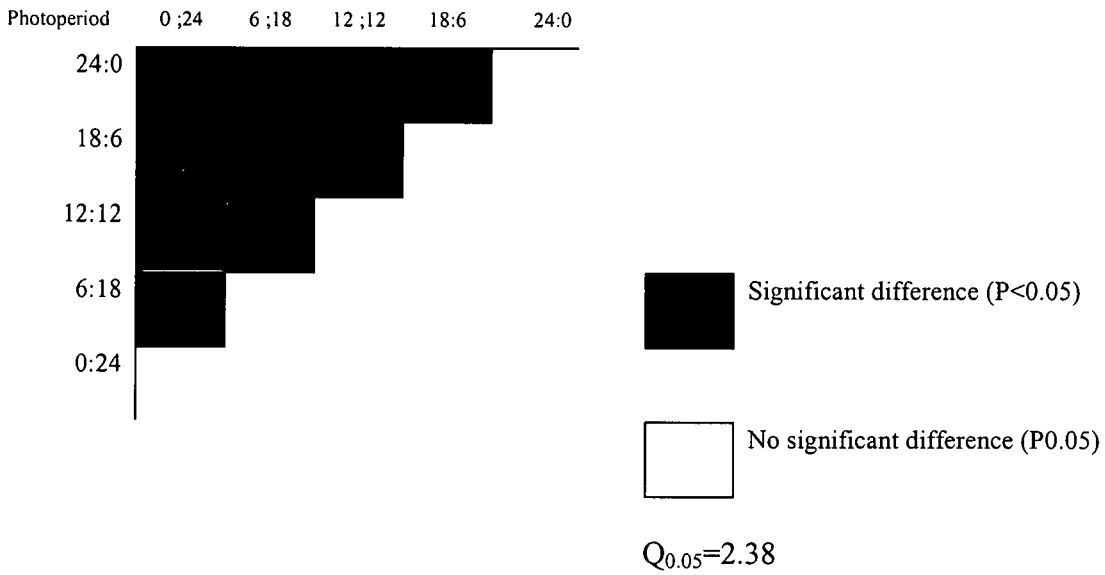
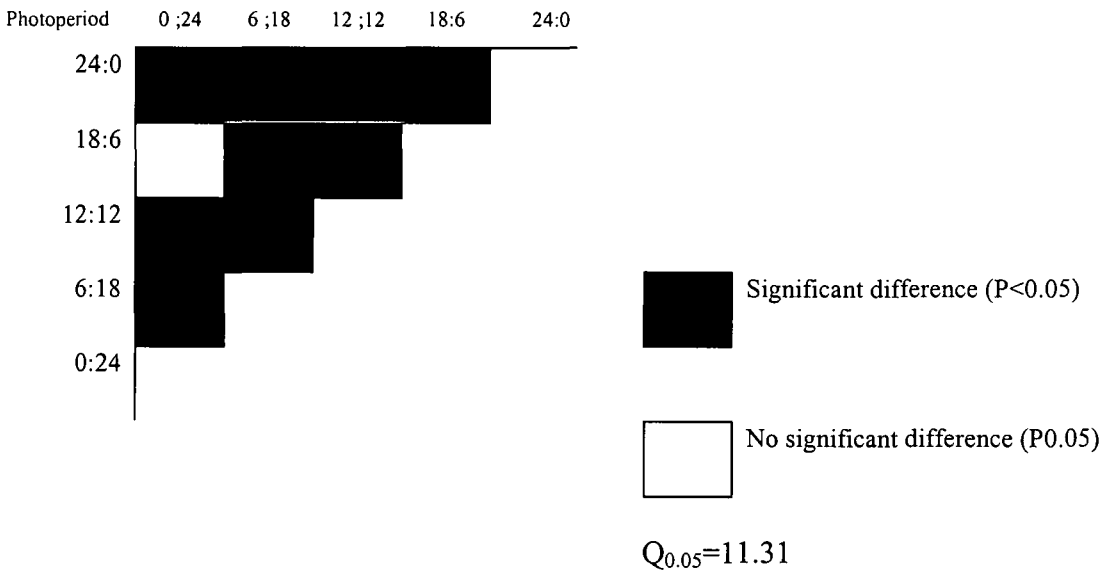


Figure A5.5: A schematic presentation of the significant differences in the total number of eggs oviposited by *Coproica vagans* at different photoperiods.

Table A5.6: Analysis of variance of the total number of eggs produced by *Coproica hirtula* adults at different photoperiods.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	158186.4	4	39546.6	5.97745653	0.00060364	2.57873722
Error	297718.1	55	6615.95778			
Total	455904.5	59				



$Q_{0.05}$=11.31

Figure A5.6: A schematic presentation of the significant differences in the total number of eggs oviposited by *Coproica hirtula* at different photoperiods.

Table A5.7: Results from t-tests (indicated by P-values) in comparing development times between *Coproica vagans* and *Coproica hirtula* of all stages at different constant temperatures.

Temperature(°C)	12	18	24	30	36
Oviposition period	0.999	0.021*	0.046*	0.048*	0.326
Total number of eggs	0.333	0.037*	0.030*	0.033*	0.032*

(* indicate significant difference [P<0.05])

Table A5.8: Results from t-tests (indicated by P-values) in comparing development times between *Coproica vagans* and *Coproica hirtula* of all stages at different photoperiods.

Photoperiod (L:D)	0:24	6:18	12:12	18:6	0:24
Total number of eggs	0.805	0.009*	0.029*	0.028*	0.039*

(* indicate significant difference [P<0.05])

CHAPTER 6

THE INFLUENCE OF DIFFERENT DUNG TYPES ON THE DEVELOPMENT AND SURVIVAL OF *COPROICA VAGANS* AND *COPROICA HIRTULA*

6.1 INTRODUCTION

Different Sphaeroceridae species have different habitat preferences and breed in different types of decaying matter (Pitkin, 1989). Oviposition and larval development of *C. vagans* and *C. hirtula* are generally restricted to bovine faeces at feedlots, although there are several isolated reports of breeding in other dung types (Pitkin, 1986). According to Richards (1930) most of the "dung haunting species" in Britain are not restricted to dung of any particular animal.

In this regard Fredeen & Taylor (1964) described a situation where *L. caenosa* used human excrement as a larval medium by infesting and breeding in sewage disposal tanks in Saskatchewan, Canada. *Leptocera caenosa* was also reported from blocked sewage drains in Ireland (Good & Sleeman, 1988). Papp (1985) listed the occurrence of 15 Sphaeroceridae species, including several *Coproica* species, on sheep droppings in Hungary. Richards (1930) recorded 29 Sphaeroceridae species on dung and mentioned that species such as *Spelobia crassimana* (Haliday), *Copromyza equina* (Fallèn) and *Sphaerocera subsultans* Linnaeus were common on horse manure, but rare on cow dung (Richards, 1930). Hammer (1941) observed that few *Coprophila pusilla* (Meigen) and *C. ferruginata* individuals were found on cow dung in Denmark, whilst they occurred in thousands on horse dung. Coffey (1966) reared *C. vagans* from swine, cow, horse, chicken and mink dung in the USA. Hafez (1949) recorded seven species, including *C. vagans* and *C. hirtula* breeding in camel dung in Egypt, while both species were also recorded on bear excrement in the Czech Republic during succession studies on adult

Sphaeroceridae (Rohacèk 1983). Conn & Marshall (1991) recorded *L. caenosa* and *Spelobia tenebrarum* (Aldrich) from guano depositions in a bat cave in Kentucky, USA.

Laurence (1955), Morgan & Graham (1966), Bay *et al.* (1969) and Fredeen & Glen (1970) all emphasized that cattle diet plays an important role in determining the efficiency of the larval rearing media. This is because some diets, due to the large amounts of fibre in it, tend to make the texture of the dung much coarser and thus less moist than other diets like alfalfa and sorghum, which produced soft, moist dung.

The primary questions of these studies were as follows:

(1) What is the survival rate of the different developmental stages in the life-cycle of *C. vagans* and *C. hirtula* on dung of different animals, as well as on the three phases of feedlot dung?

(2) What is the chemical composition of these dung types and would this have any influence on the occurrence and development of Sphaeroceridae?

6.2 MATERIAL AND METHODS

6.2.1 Development and survival in different dung types

Eight different dung types, cattle (three feedlot phases), sheep, horse, elephant, rhinoceros and buffalo dung were used. Cattle and sheep dung was collected at Blokhuis feedlot near Harrismith, while horse, elephant, rhino and buffalo dung was collected from the Bloemfontein zoo. Sheep dung was crushed into a finer texture and not kept in its original hard, round pellet form. The different types of dung were put into Apex vials No. 8 to a depth of one centimetre and the vials were closed with perforated stoppers to allow air ventilation. The moisture content of the dung inside the vials was kept at

approximately 80% by adding distilled water to the dung every second day. The experiments were conducted in incubators set at 24 ± 1°C with a day-night cycle of 12 hours light and 12 hours dark. Before the onset of the experiment the vials containing the dung were preconditioned by exposing them to a temperature of 24 ± 1°C for 24 hours. Containers filled with distilled water were put inside these incubators to maintain a relative humidity of approximately 65%. This procedure was followed for all four developmental stages of Sphaeroceridae, which were tested during these experiments. Each experiment consisted of 10 replicates and was repeated three times for each of the two species used. Observations were made every 12 hours.

Individual females from the two laboratory colonies (F2) of *C. vagans* and *C. hirtula* were introduced to the prepared Apex vials and allowed to oviposit on the eight different dung types. The females were removed after 24 hours and the number of eggs that were oviposited was determined. The eggs were left undisturbed inside the Apex vials until hatching was completed, after which the percentage hatching was calculated.

Larvae from a specific dung type were pooled. From these, eight groups of 50 first instar larvae from each dung type were introduced into each of the Apex vials containing the eight different dung types. Care was taken to put the larvae on the same dung type on which the eggs were initially oviposited. Larval duration was calculated from the time that the eggs hatched until the larvae were ready to pupate. Larvae that were ready for pupation slowed down their movement considerably and became short and oval shaped. Twenty-five pupae were introduced to each of the Apex vials containing the eight different dung types. These pupae originated from the larvae that completed their development in the previous set of Apex vials. The pupae were transferred to the same dung types where the larval development took place. Unfortunately it was not always possible to collect 25 pupae from the larval experiment because some of the dung types resulted in very low larval survival rates. Therefore additional pupae then had to be

taken from the laboratory colonies. However, care was taken to select "fresh" pupae from the laboratory colonies - *i.e.* pupae not older than 12 hours.

Adult survival was determined by individually placing 24-hour-old adults from the laboratory colonies into the Apex vials containing the eight different dung types. Survival of the flies was calculated from commencement of the experiment until all the flies had died. The 24-hour period from inclusion until commencement of the trial was also included in the calculations. Any eggs that were produced by these flies were removed and discarded.

In a separate experiment manure was omitted from the vials and the eggs and pupae were placed on filter paper over a piece of wet cotton wool directly after oviposition and at the onset of pupation. The purpose of this was to determine whether the absence of manure would have any effect on the hatching of the eggs or on pupal development.

6.2.2 Chemical content of the dung

Chemical analysis of the dung was done to establish whether the differences in survival of the immature and adult stages on the eight different dung types could be related to the chemical composition of the dung. Initially it was thought that the nitrogen content of the dung might be of some importance. That would have explained the absence of flies from the phase 3 dung at Blokhuis feedlot. All dung was dried in sunlight for about a month after which it was ground to a fine powder.

The chemical analyses that were done are listed below and were carried out according to standard analytical procedures described by the authors mentioned in brackets.

(i) pH (McLean, 1982)

(ii) Cations (Thomas, 1982)

(iii) Phosphate content (Olsen & Sommers, 1982)

(iv) Nitrogen content (Bremner & Mulvaney, 1982)

(v) Organic content (Schnitzer, 1982)

6.3 RESULTS AND DISCUSSION

6.3.1 Development and survival in different dung types

Eggs hatched on all dung types. The average hatching percentages of both *C. vagans* and *C. hirtula* on all dung types varied between 55% and 90% (Fig. 6.1). For *C. vagans* the lowest hatching percentage was 60 ± 5.2% and this occurred on horse dung, while the lowest hatching percentage for *C. hirtula* was also 55 ± 5.1%, also on horse dung. On phase 1 feedlot dung and sheep dung, hatching percentages of *C. hirtula* eggs were 60%. None of the other hatching percentages was below 60%. The highest hatching percentages were 90 ± 6.7% for *C. vagans* and 80 ± 5.9% for *C. hirtula*, both on phase 2 feedlot dung (Fig. 6.1).

Analysis of variance ($F_{56;7}$=42.05) showed that significant differences ($P<0.05$) existed in the percentage hatching of *C. vagans* eggs on the different dung types (Table A6.1). Tukey's test ($Q_{0.05}$=14.95) indicated that egg hatching on phase 2 dung was significantly higher compared to those on the other dung types (Fig. A6.1). Significant differences were shown between hatching of eggs on all the different dung types except between elephant and buffalo dung and also between rhino and sheep dung, where no significant differences were found (Fig. A6.1). In the case of *C. hirtula*, analysis of variance ($F_{56;7}$=34.88) indicated that significant differences ($P<0.05$) also existed in the percentage egg hatching on different dung types (Table A6.2). With Tukey's test ($Q_{0.05}$=23.31) significantly more eggs hatched on cattle dung (Phase 2) than on the other dung types. However, no significant differences could be found in egg hatching between phase 1 cattle dung and sheep dung or between phase 3 cattle dung and buffalo dung

(Fig. A6.2). Egg hatching on horse dung was also significantly lower than on any of the other dung types (Fig. A6.2). A t-test was also used to compare the hatching percentages of *C. vagans* and *C. hirtula* eggs on the different dung types. This was done by statistically comparing the mean of two samples. Significant differences ($P<0.05$) were found between the two species at all the dung types except on the buffalo dung (Table A6.9).

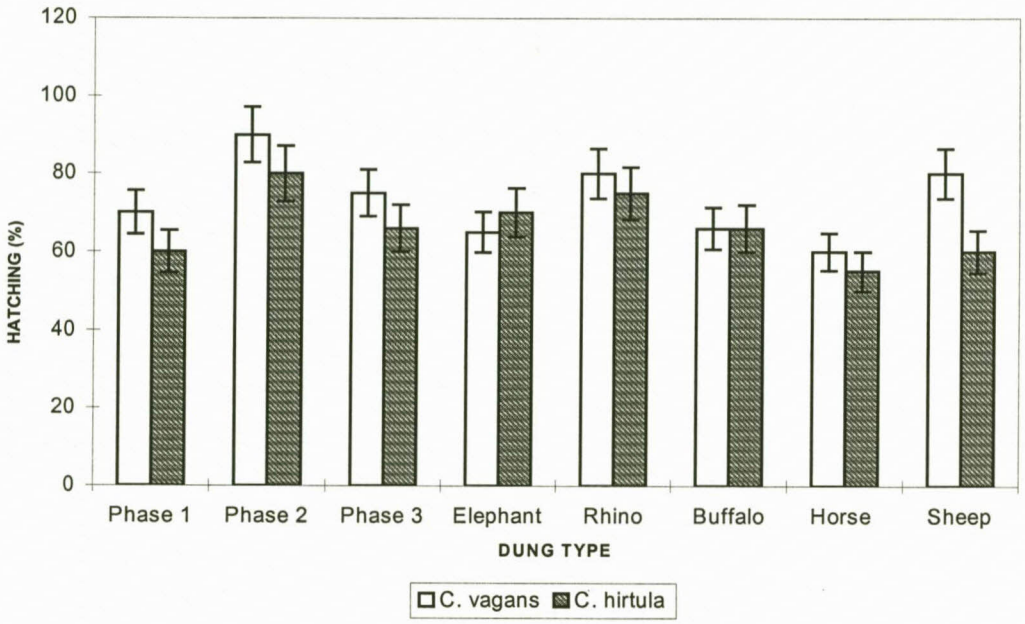


Figure 6.1: Average hatching percentages of *Coproica vagans* and *Coproica hirtula* eggs on eight different types of dung. (Phase 1-3: Cattle dung).

The results provided conclusive evidence that larval breeding medium has no effect on development or hatching of Sphaeroceridae eggs. Additional evidence also came in the form of a separate experiment in which dung was omitted from the vials and where the eggs were placed on wet filter paper and cotton wool. Similar hatching percentages (above 60%) compared to those eggs which were oviposited onto the manure were shown. Dung is obviously important as a food resource for the larvae, but this clearly demonstrates that neither composition nor the type of manure played any role in

determining egg development or percentage hatching of the eggs. Certain factors such as temperature and moisture content of the dung would be much more important in ensuring successful hatching of eggs (see 3.3.2.1 & 4.3.3.2). In nature oviposition choice, focussed on survival of a progeny, would probably also avoid dry and coarse dung types. Thomsen & Hammer (1936) found in their studies on the breeding media of some flies, that most flies such as *M. domestica*, *S. calcitrans* and *Fannia* species breed in a variety of dung types. No mention was made that the breeding media affected either development or hatching of the eggs, although it was mentioned that temperature and moisture content had a negative influence on the hatching of fly eggs (Thomsen & Hammer, 1936).

Cattle dung of the three different phases from Blokhuis feedlot (see 6.2.1) had no adverse effect on larval development of Sphaeroceridae. Larval survival on the three phases of feedlot dung varied between 63% and 77% for *C. vagans* and between 61% and 75% for *C. hirtula* (Fig 6.2). Survival of *C. vagans* larvae was constantly better than those of *C. hirtula* on all three phases cattle dung. Larvae of *C. vagans* and *C. hirtula* developed successfully in elephant dung (62 ± 3.8% and 55 ± 3.4% respectively), which explains why so many flies were present on the elephant dung in the zoo. *Coproica vagans* and *C. hirtula* larvae also survived successfully in sheep dung (63 ± 3.1% and 58 ± 3.7% respectively) (Fig. 6.2), which proved that sheep dung present at feedlots could be a potential breeding medium for Sphaeroceridae. However, this would only be possible if the sheep dung was not kept in pellet form, but trampled to a fine texture, similar to the texture of the sheep dung used in this experiment. Larval development and survival in horse, rhino and buffalo dung were only between 1.5% and 5% for both species (Fig. 6.2).

Analysis of variance ($F_{88;7}$=36.37) showed significant differences ($P<0.05$) in survival of *C. vagans* larvae on the different dung types (Table A6.3). Tukey's test ($Q_{0.05}$=20.21) indicated that larval survival on rhinoceros, buffalo and horse dung was significantly

lower than on the other dung types, although rhino and horse dung did not differ significantly from each other (Fig. A6.3). Survival on phase 2 dung was also significantly higher compared to the rest of the dung types (Fig. A6.3). No significant differences in larval survival occurred between phase 3, elephant or sheep dung and also not between buffalo and horse dung (Fig. A6.3). As far as *C. hirtula* is concerned, an analysis of variance ($F_{88;7}$=25.85) indicated that significant differences ($P<0.05$) also existed in larval survival on different dung types (Table A6.4). With Tukey's test ($Q_{0.05}$=17.88) significantly more larvae survived on cattle dung (Phase 1-3), elephant and sheep dung than on rhino, buffalo and horse dung (Fig. A6.4). No significant differences in larval survival could be found between those that developed on elephant and sheep dung or between those on rhino and horse dung (Fig A6.4). A t-test was also used to compare the mean larval survival between *C. vagans* and *C. hirtula* larvae on the different dung types. Significant differences ($P<0.05$) in larval survival were found at all the dung types except on the rhino dung (Table A6.9).

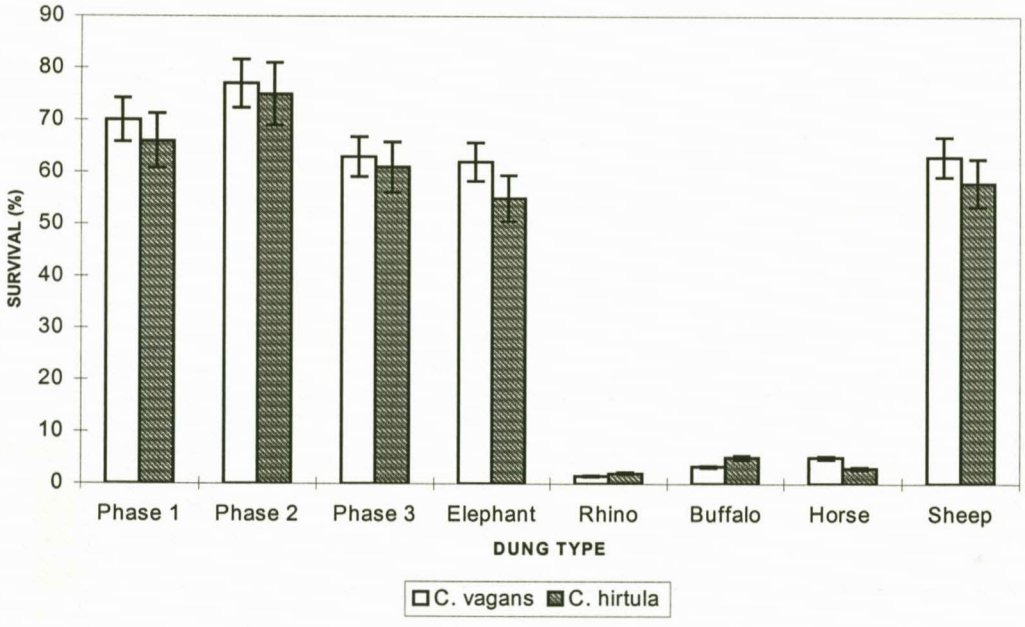


Figure. 6.2: Percentage survival of *Coproica vagans* and *Coproica hirtula* larvae in eight different types of dung. (Phase 1-3: Cattle dung).

Eight different dung types were included in these experiments in which sphaerocerid larval survival was tested. Observations were made at the Blokhuis feedlot near Harrismith and at other chosen dung collecting sites which revealed several interesting phenomena. At the feedlots, newly arrived cattle are fed on a conditioning diet (phase 1) for 75 days. This phase 1 diet consisted mainly of cut grass from local fields that yielded drier dung in the phase 1 camps than in the phases 2 and 3 camps. In this context Cole and Hutcheson (1988) emphasized the importance for all newly arrived animals to be fed on a conditioning diet to meet the nutritional requirements of the animals. This was followed by a second diet (phase 2) for 40 days. From 115 days post-arrival until they are ready for the market, the cattle receive a phase 3 diet. Phases 2 and 3 consisted mainly of maize and grain in much finer form with additional additives to stimulate cattle growth. These diets produced very soft, moist dung. The pH of phase 3 dung was very low with a high nitrogen content. Low numbers of Sphaeroceridae were observed in the phase 3 camps, while large swarms were present at the conditioning phase 1 camps and at the phase 2 camps.

Larval development and survival of Sphaeroceridae in the phase 2 dung, where the animals were already receiving a more complex diet, were significantly better than in the phase 1 dung, where animals were fed on the conditioning diet (see Fig. 6.2). These findings are in agreement with those by Bay *et al.* (1969) who found, in their studies on face flies in the USA, that soft, moist cattle faeces were produced from roughage diets supplemented with grain, while hard, pelleted faeces resulted when prairie hay was fed exclusively. They also found that faeces from animals fed exclusively on alfalfa hay were moist but firm, and that the survival of face fly larvae on these types of dung was better than on the prairie hay faeces (Bay *et al.*, 1969). Larval survival on cattle feedlot dung furthermore showed that it would probably be very difficult to control Sphaeroceridae flies by changing the chemical composition of the dung through supplementations to the diet. However, fly control had been done by scientists when

anti-parasitic drugs such as ivermectin was administrated to cattle (Sommer *et al.*, 1992 ; Halley *et al.*, 1993).

Although larval development and survival in sheep dung proved to be above 55%, the dung used in these experiments was not kept in its original pellet form, which could imply that the flies at the feedlot cannot utilize sheep dung pellets as a breeding medium. This corresponds with the findings of Bay *et al.* (1969) who stated that the failure of face flies to propagate successfully in fresh sheep and deer dung may be attributed to their pelleted form and lower moisture content. They were able to show that both larval development and egg oviposition by adult flies were successful in reconstituted samples. Edwards (1991) also stated that small pellets dried out much faster than solid pats, which poses a further problem for larvae which use sheep or deer dung as a breeding medium. However, during summer, conditions at the sheep section of the feedlot frequently became very wet because of heavy rainfall. Together with the animals continually trampling the dung, the medium was then turned into a mass of wet, soft dung. Sphaeroceridae flies would then be able to utilize the sheep dung in this form, as was proven by the results of these experiments.

Larval survival in horse, rhino and buffalo dung was severely limited. The reason for this is unknown, but it could be attributed to the higher fibre contents of these dung types that made it unsuitable for any larval development. These results are in agreement with those of Bay *et al.* (1969) who also stated that it appeared as if the diet of an animal and thus also the fibre content of the dung influenced both oviposition preferences and larval development of face flies negatively. The fact that the larvae did not survive in rhinoceros or buffalo dung could also explain the absence of these flies at the rhinoceros and buffalo cages at the zoo. Laurence (1955) also stated that different types of dung produced by several animals differ in physical composition. In England, cattle that were fed mainly on hay and roots during the winter, deposited dung that was coarser and contained less fluid than dung deposited by cattle that were grazing during the summer,

when the dung was softer with a higher moisture content (Laurence, 1955). The inclusion of large amounts of dry material in the diet also contributed to the production of drier dung. These findings are in agreement with those of Morgan & Graham (1966) who found that faeces from animals fed prairie hay and green oats were considerably drier than those fed on alfalfa and sorghum hay diets. Larger populations of horn flies were produced from the latter diet (Morgan & Graham, 1966).

Pupal emergence occurred on all the dung types that were used in this experiment. In fact, the percentage pupal survival for both species in the different dung types were very high and varied between 65% and 90% (Fig. 6.3). The lowest pupal survival was 65 ± 4.9% for *C. vagans* and 70 ± 5.6% for *C. hirtula*, both on rhino dung (Fig. 6.3). It is interesting to note that although the lowest pupal survival for Sphaeroceridae occurred on rhino dung, egg survival and hatching on rhino dung was generally good. The highest pupal survival for *C. vagans* pupae was 90%, which occurred on phase 1, elephant, horse and sheep dung. For *C. hirtula*, the highest survival was 85% on phase 2 feedlot dung (Fig. 6.3).

Although analysis of variance ($F_{48;7}$=8.92) showed significant differences ($P<0.05$) in survival of *C. vagans* pupae on the different dung types (Table A6.5), Tukey's test ($Q_{0.05}$=2.44) indicated that pupal survival on rhino dung was significantly lower compared to the rest (Fig. A6.5). Pupal survival on buffalo dung also differed significantly from all the rest, but no significant differences in pupal survival were shown between the those that developed on phase 1, elephant, horse or sheep dung or between those on phase 2 and phase 3 cattle dung (Fig. A6.5). In the case of *C. hirtula*, analysis of variance ($F_{48;7}$=2.30) also indicated significant differences ($P<0.05$) in pupal survival on the different dung types tested (Table A6.6). Tukey's test ($Q_{0.05}$=1.81) furthermore showed that pupal survival on rhino dung was significantly lower than on the rest of the dung types, while it also proved to be significantly higher on phase 2 dung compared to the rest of the dung types (Fig. A6.6). No significant differences existed in

pupal survival between phase 1, phase 3, buffalo or horse dung or between elephant and sheep dung (Fig. A6.6). A t-test was used to compare pupal survival between *C. vagans* and *C. hirtula* by comparing the mean of two samples. Significant differences ($P<0.05$) in pupal survival were shown to exist between the two species on all the dung types, with the exception of phase 3 dung (Table A6.9).

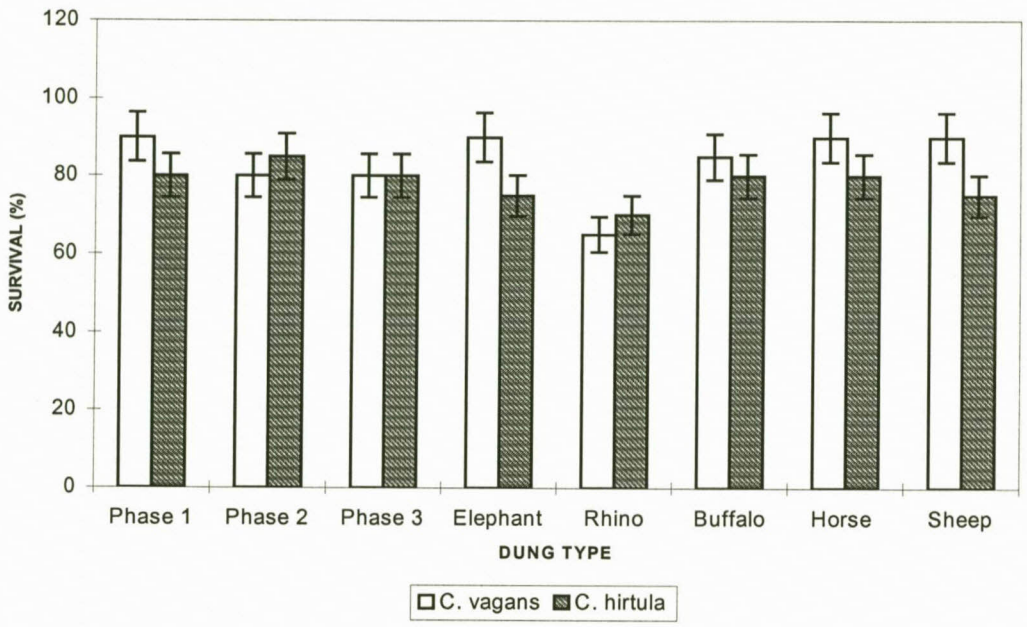


Figure 6.3: Percentage survival of *Coproica vagans* and *Coproica hirtula* pupae on eight different types of dung. (Phase 1-3: Cattle dung).

From the results it is clear that various dung types did not affect the development of sphaerocerid pupae negatively, and that adult emergence will occur normally provided that favourable temperature and humidity conditions prevail. However, this does not correspond with the findings of Bay *et al.* (1969) who stated that a high percentage pupal emergence resulted from faeces of animals whose feeding was supplemented with grain. Faeces passed from animals maintained exclusively on prairie hay yielded a lower percentage of pupal emergence (Bay *et al.*, 1969). This could again be contributed to the effect of the prairie hay dung had on the larvae and that the minimum percentage pupal

emergence could only be a result of lower larval survival. Bay *et al.* (1969) did not mention any further effect of breeding medium on face fly pupal development and survival, probably because neither eggs nor pupae depended on dung as a food resource. Furthermore it has been proved that the sphaerocerid pupal development can even occur in the absence of dung.

Adult flies of both species survived for 10 days and longer on all three phases of feedlot cattle dung (Fig. 6.4). In the case of *C. vagans* for instance, adults survived on average up to 17 days on phase 2 feedlot dung and on sheep dung. Adult flies also survived 9 days and longer on the other dung types, with the exception of rhinoceros and horse dung, where the longevity of adult sphaerocerids dropped to between 2 and 7 days respectively (Fig. 6.4). The survival of *C. hirtula* adults on rhinoceros and horse dung was also not more than 5 days (Fig. 6.4).

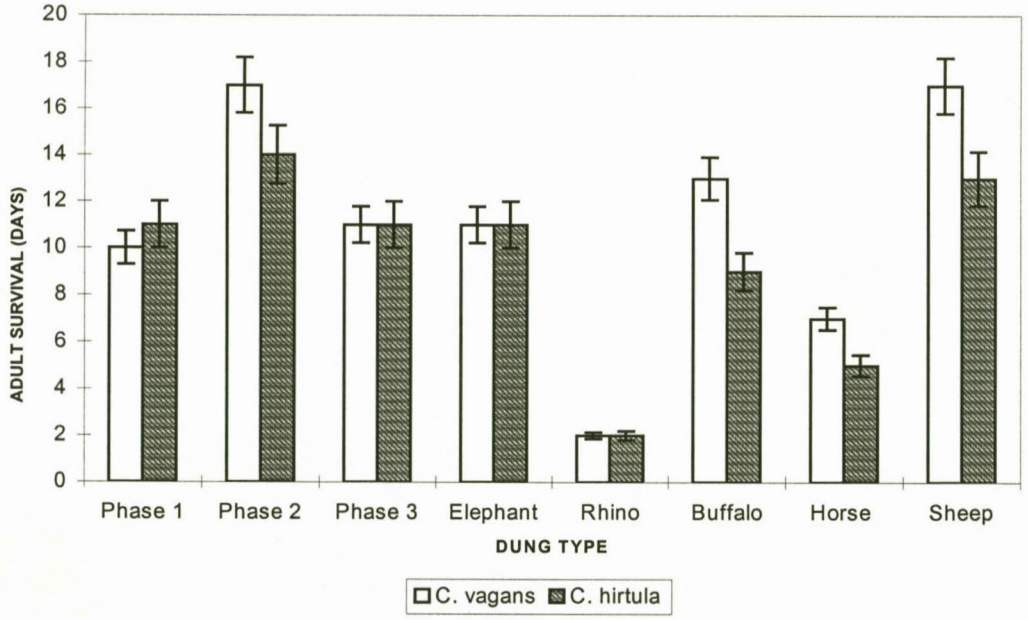


Figure 6.4: The survival period of adult *Coproica vagans* and *Coproica hirtula* flies on eight different types of dung. (Phase 1-3: Cattle dung).

Analysis of variance ($F_{72;7}$=26.77) showed significant differences ($P<0.05$) in survival rates of *C. vagans* adults on the different dung types that were used (Table A6.7) Tukey's test ($Q_{0.05}$=13.59) indicated that the longevity of *C. vagans* adults on rhinoceros and horse dung was significantly shorter compared to adult survival on the other dung types (Fig. A6.5). However, no significant differences in adult survival could be found between those that developed on phase 2 and sheep dung, or between those on phase 3 and elephant dung (Fig. A6.7). In the case of *C. hirtula*, analysis of variance ($F_{72;7}$=11.19) also indicated that significant differences existed in adult survival on different dung types (Table A6.8). Tukey's test ($Q_{0.05}$=4.74) showed that adult longevity on rhino and horse dung was again significantly lower compared to survival rates on the other dung types, but it also differed significantly from each other (Fig. A6.8) No significant differences in adult survival could be found between phase 1, phase 3 and elephant dung (Fig. A6.8). In order to compare statistically between the mean adult survival of the two species, a t-test was used. This indicated that significant differences existed between *C. vagans* and *C. hirtula* on all the dung types except on phase 3, elephant or rhino dung (Table A6.9).

The tendency in different species of Sphaeroceridae to prefer dung of a particular species of animals has been observed by various researchers. Richards (1930) recorded the abundant occurrence of *S. crassimana* on horse manure in Britain and its absence or rare occurrence on cow dung. Thomsen & Hammer (1936) have similarly shown that the greatest numbers of *Leptocera* species emerged from horse manure in Denmark, while cow dung yielded only a few species. Hammer (1941) also pointed out that very few *C. pusilla* and *C. ferruginata* were found on cow dung in Denmark, while they occurred in their thousands on horse droppings. Conditions between countries in the Northern and Southern Hemispheres differ considerably in terms of climate, feeding pastures and dung composition, and careful considerations should be given when comparisons are made between species of the same family. Great numbers of *S. subsultans* were also reported from calf, cow, horse and pig dung (Thomsen & Hammer, 1936). In Egypt horse dung

seemed to attract the ovipositing females of *C. ferruginata*, *C. vagans* and *Spelobia puerula* (Rondani) more than any other kind of dung (Hafez, 1949). *Leptocera curvinervis* (Stenhammer), *Leptocera fuscipennis* (Haliday) and *E. nigerrima* emerged from various kinds of dung in relatively large numbers, while the latter species seemed to prefer cow dung for oviposition (Hafez, 1949). *Musca domestica* and *S. calcitrans* were recorded from pig dung, calf stables and horse boxes (Thomsen & Hammer, 1936). Contrary to these findings from the literature, results from the present study indicated that the survival of adult Sphaeroceridae was not successful on all dung types that were included in the experiments. For instance, adult sphaerocerid survival was badly affected on rhino dung and to a certain degree on horse dung as well. The reason for this was most probably the higher fiber content which caused the dung to be coarser and therefore provided less nutrition to the flies, which consequently resulted in shorter survival times for adult flies. This is also the view of Bay *et al.* (1969), who found that fewer face fly eggs occurred in the drier horse and sheep dung, demonstrating the importance of moisture content in determining an oviposition site by adult flies. Furthermore they stated that face flies did not oviposit readily in horse dung, probably because of the coarse texture of the dung (Bay *et al.*, 1969).

Observations made at the feedlot showed that adult sphaerocerids avoided phase 3 dung, but the reason as to why they did, is unknown. Since these camps were permanently soaked during the wet summer months, it could be that phases 2 and 3, in comparison to the phase 1 camps, were too wet for the flies. With the cattle continually tramping on the dung, conditions became extremely unfavourable for flies to feed and breed, despite the fact that adult survival on this dung was very good in laboratory experiments. Phase 1 camps on the other hand were normally not as crowded with cattle and the drier hay diet that these animals received as food made the dung and the camps much drier than the rest of the feedlot.

6.3.2 Chemical content of the dung

During the chemical analyses of the eight dung types the pH-values varied between 6.4 and 7.7 with an average of 7.3 (Table 6.1). The inorganic content of the dung *i.e.* Na^+, K^+, Ca^{++}, Mg^{++}, P and N, only showed slight differences between the eight types tested (Table 6.1). However, the dissolving and exchangeable cations (Na^+, K^+, Ca^{++}, Mg^{++}) and P were present in such small amounts, that it is doubtful whether it will have any effect on the Sphaeroceridae larval survival in the dung. The highest Na^+-content was found in phase 1 cattle dung, while the Na^+-content was extremely low in buffalo, horse and phase 2 dung. The highest K^+-content was found in sheep dung and the lowest in phase 2 dung (Table 6.1). The highest Ca^{++}, Mg^{++} and P contents were found in phase 2 dung and the lowest in buffalo dung. The highest N content was found in phase 3 dung which could have been expected since the cattle in the phase 3 camps at Blokhuis feedlot were fed on a special nitrogen rich diet which lowered the pH value of the dung. The lowest N content was found in buffalo dung. Another component of dung that was also very important for the development and survival of coprophagous insects is its organic component. The percentage organic matter present in the eight dung types was relatively high (Table 6.1). The highest was 88% and was found in rhino dung and the lowest was 55% in the sheep dung. It therefore seems as if dung with a higher fibre content had a negative effect on the survival of the larvae, at least in the case of *C. vagans* (Fig. 6.3).

Chemical analysis of the different dung types showed that the three phases of feedlot dung differed only slightly with regards to inorganic content (Table 6.1). Both adult flies and larvae were able to utilize all three types of feedlot dung, as well as elephant and sheep dung, but their survival was poor in the other three dung types tested. Bay *et al.* (1969) stated that although roughage-exclusive diets yielded drier faeces and subsequently also a decrease in the production of flies, their decreased productivity could not be entirely attributed to lower moisture contents. The influence of chemical

composition such as the organic component of faeces on face fly development should also be taken into account (Bay *et al.*, 1969).

Table 6.1: Chemical composition of eight different dung types.

No	pH	Na^{++}	K^{+}	Ca^{++}	Mg^{++}	P	N	Org
Ph1	7.2	1.20	0.81	1.54	0.67	0.58	2.42	86
Ph2	6.8	0.07	0.37	1.67	0.70	0.59	2.60	82
Ph3	6.4	0.11	0.58	1.35	0.63	0.57	3.12	79
Elep	7.5	0.14	1.53	1.23	0.31	0.29	2.25	82
Rhin	7.7	0.51	0.54	0.56	0.38	0.48	1.42	88
Buf	7.6	0.03	0.64	0.21	0.15	0.16	1.09	74
Hor	7.6	0.05	0.55	0.64	0.16	0.27	1.13	80
She	7.5	0.18	3.70	1.03	0.56	0.38	2.22	55

$\bar{x}$ 7.3 (All chemicals measured in ppm; organic component in %)

Key: P1 - Phase 1; P2 - Phase 2; P3 - Phase 3; Elep - Elephant: Rhin - Rhinoceros; Buf -Buffalo; Hor - Horse; She – Sheep.

Survival of larvae and adult flies on rhino dung was very low, and the chemical analysis of dung revealed that the rhino dung was lower in nitrogen and contained slightly more fiber than cattle feedlot dung. It thus seems as if these two components were most important in determining survival of Sphaeroceridae in dung. This is in line with the findings by Edwards (1991), who mentioned that nitrogen is one of the most important elements in the dung of herbivores in determining the survival of dung breeding insects such as dung beetles and the larvae of several coprophagous flies. Current results clearly showed that the suitability of dung as food for sphaerocerid larvae was influenced by the species of animal that produced it. Edwards (1991) indicated that for herbivores, interspecific variability in dung characteristics arises from the major dichotomies in herbivore feeding and digestion, *e.g.* grazing *vs.* browsing and rumination *vs.* non-

rumination. Body size of herbivores places further constraints on the nutritional requirements and feeding ecology (Demment & Van Soest, 1985). These sources of variation result in dung that differs in characteristics such as texture and size of droppings, and in water, nitrogen and fiber content (Demment & Van Soest, 1985). In addition, Greenham (1971) found that rainfall caused an increase in nitrogen content of dung. On the other hand, Greenham (1971) concluded that nitrogen content of dung is not a particularly good measure of the potential increase of bush fly in Australia. However, Chamberlain & Matter (1986) successfully used calcium cyanamide fertilizer to control stable flies, and stated that the additional nitrogen in the calcium cyanamide was responsible for the killing of stable fly larvae.

Because different dung types were used during these experiments, it was important to keep in mind that differences in characteristics of cattle, elephant, rhino, buffalo, horse and sheep dung also reflect differences in feeding ecology of these herbivores. Buffalo and rhino dung for instance, were coarse textured and contained less nitrogen than dung of most of the other species. This could be a reflection of the buffalo and rhino's preference for older grass and less thorough digestive processes, as was suggested by Edwards (1991). Greenham (1971) showed that the main components of dung are: undigested food residues, including plant cell walls and lignified tissue; products of the gut flora and fauna, including intact and disintegrated micro-organisms; secretions and cellular debris from gut mucosa and the excretory products of the beast's metabolism. Dung is thus a residue of pasture after it has interacted with the digestive processes of the ruminant animals and its symbiotic microorganisms (Church, 1969). The most important factor affecting the composition of pasture plants is their degree of maturity (Whittet, 1964). With advancing season and growth stage a wide variety of grasses and legumes show decreases in protein content and increases in fibre and lignin (Whittet, 1964). Ruminant digestion is characteristically aided by symbiotic microorganisms which break down dietary cellulose and to a lesser extent, protein, and the number and variety of microorganisms varies (Bryant, 1951). When mature herbage is ingested, the

relatively higher proportion of cell walls and lignified tissue impedes enzyme activity, so reducing further breakdown of fibrous material and of proteins (Jarrige, 1965). As a result there is an increase in the size of solid particles in the dung and a decrease in available nitrogenous materials (Edwards, 1991). Abrasion of gut mucosa increases the size of undigested solid particles and the amount of mucus, cell debris and blood in the dung increases (Edwards, 1991).

Seasonal changes in the quantity and quality of forage could also affect the dung, and Greenham (1971) found that this had an important effect on bush fly breeding in South East Australia. Edwards (1991) also found that seasonal changes in pasture quality is a critical variable in the nutrition and feeding ecology of African grazing mammals. For instance, in the dry seasons the nitrogen content of tropical grasses can fall to a level that are insufficient to meet the protein requirements of many grazing species (Sinclair, 1975). Such changes in turn will affect the nutrition and population processes of insects that feed on herbivore dung. This has already been well documented for insects feeding on cattle dung where the variation in pasture conditions is accompanied by marked changes in the survival and reproductive rates of coprophagous beetles and flies (Ridsdill-Smith, 1986).

In conclusion, *C. vagans* and *C. hirtula* survived in most of dung types evaluated, although their life cycles in horse, buffalo and rhinoceros dung were severely disrupted. Mortality of larvae and adults in these three dung types were therefore high. All three phases of feedlot dung proved to be successful larval breeding media, even though phase 3 dung contained relatively high nitrogen levels. The development of eggs and pupae were independent on the type of medium used, since they could even develop in the absence of dung, provided that favourable temperature and moisture conditions prevailed.

6.4 APPENDIX

Table A6.1: Analysis of variance of hatching percentages of *Coproica vagans* eggs on different dung types.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	5487	7	783.857143	42.045977	4.8314E-20	2.17815455
Within Groups	1044	56	18.6428571			
Total	6531	63				

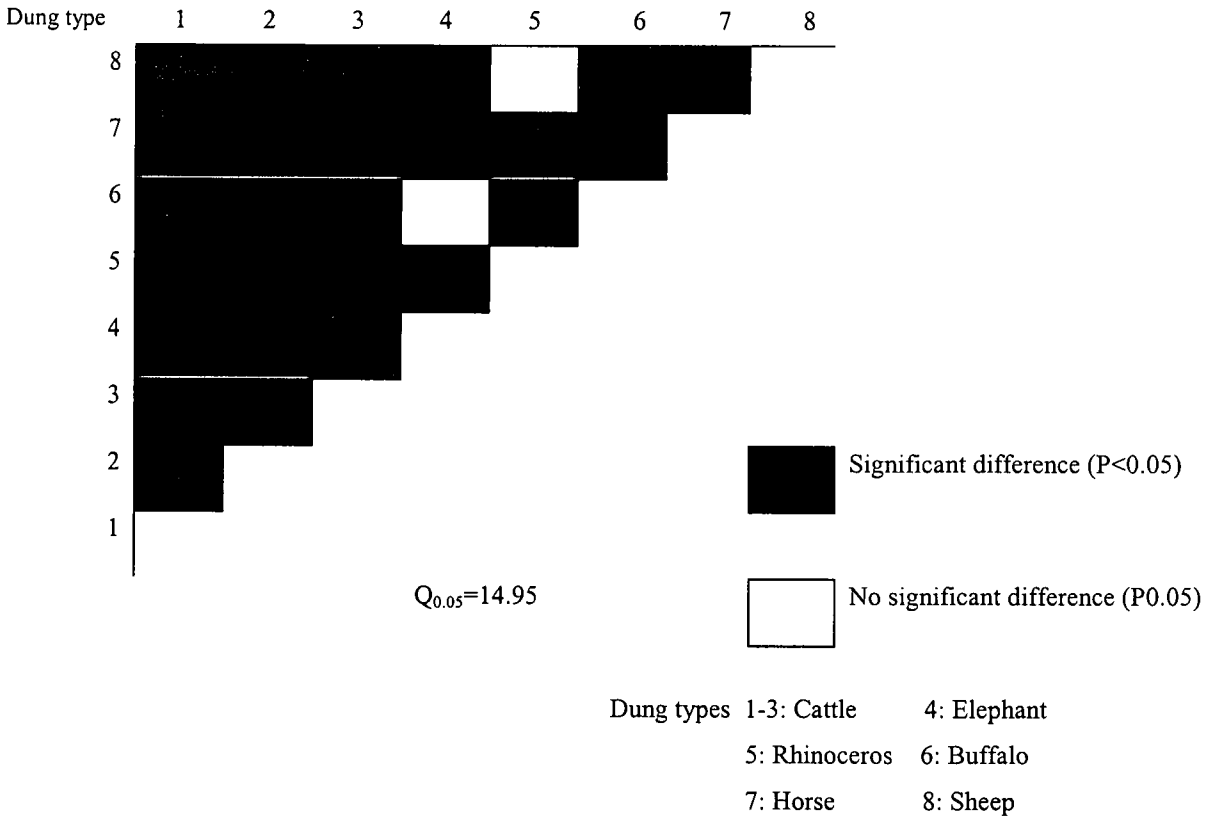


Figure A6.1: A schematic presentation of the significant differences in hatching percentages of *Coproica vagans* eggs in different dung types.

Table A6.2: Analysis of variance of hatching percentages of *Coproica hirtula* eggs on different dung types.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	3872	7	553.142857	34.8828829	3.3796E-18	2.17815455
Within Groups	888	56	15.8571429			
Total	4760	63				

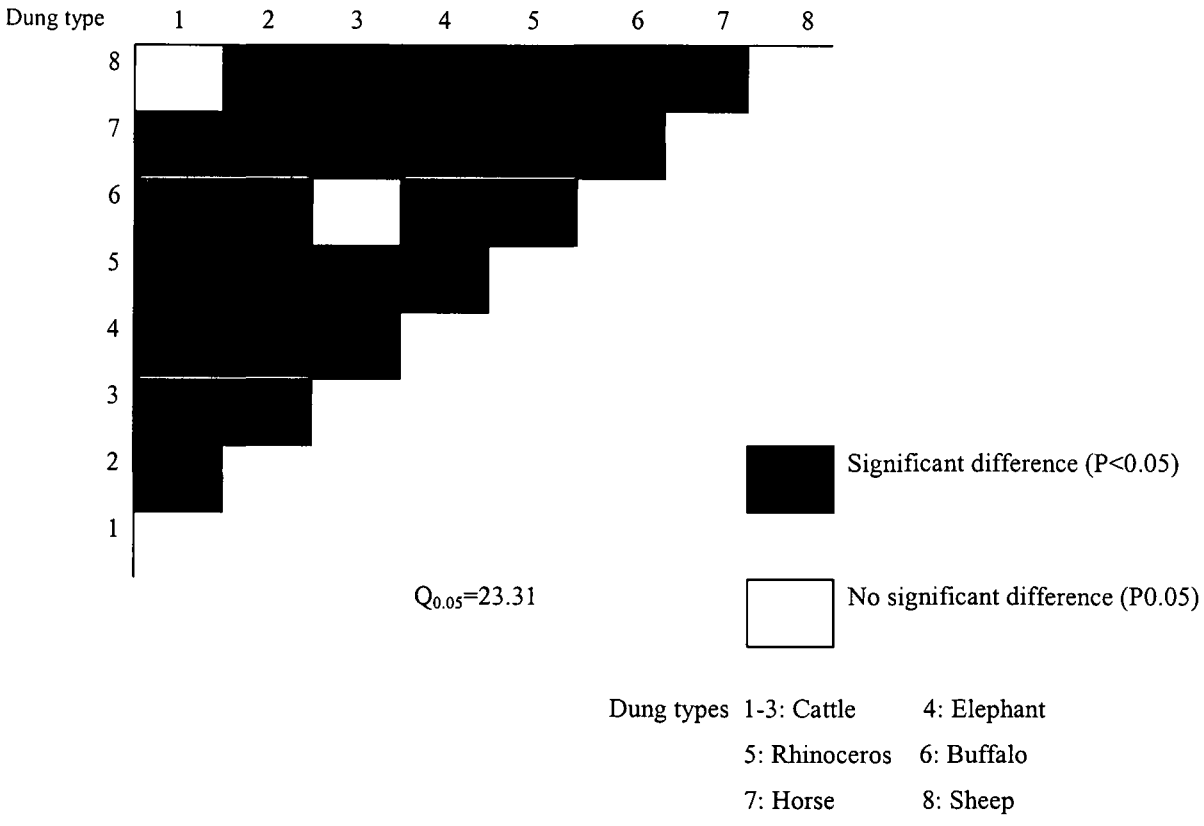


Figure A6.2: A schematic presentation of the significant differences in hatching percentages of *Coproica hirtula* eggs in different dung types.

Table A6.3: Analysis of variance of survival of *Coproica vagans* larvae on different dung types.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	54369.1086	7	7767.01551	36.3705656	1.4762E-32	2.20743601
Error	2000.40571	88	41.675119			
Total	56369.5143	95				

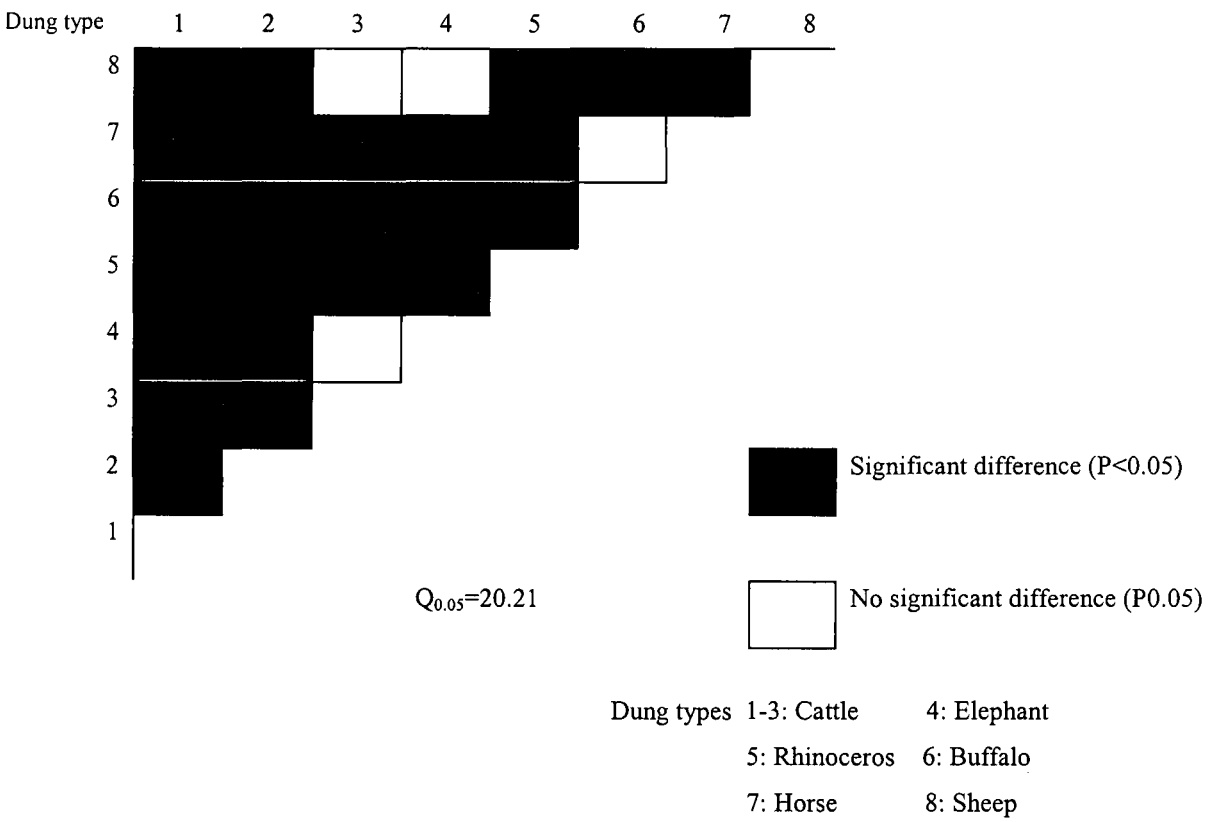


Figure A6.3: A schematic presentation of the significant differences in survival of *Coproica vagans* larvae in different dung types.

Table A6.4: Analysis of variance of survival of *Coproica hirtula* larvae on different dung types.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	50633.125	7	7233.30357	25.8541747	8.9863E-31	2.20743601
Error	2227.71429	88	46.4107143			
Total	52860.8393	95				

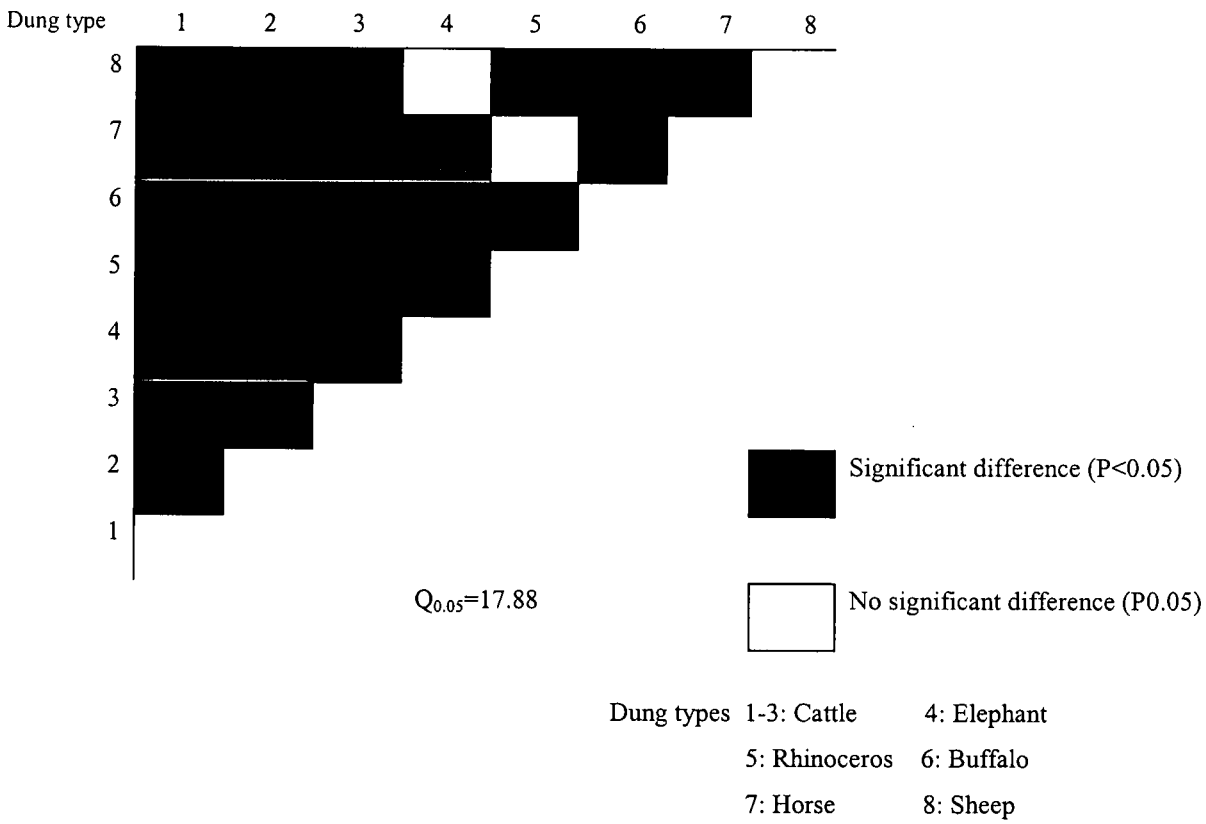


Figure A6.4: A schematic presentation of the significant differences in survival of *Coproica hirtula* larvae in different dung types.

Table A6.5: Analysis of variance of survival of *Coproica vagans* pupae on different dung types.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	3658.26786	7	522.609694	8.91897893	5.4298E-07	2.20743601
Error	2812.57143	48	58.5952381			
Total	6470.83929	55				

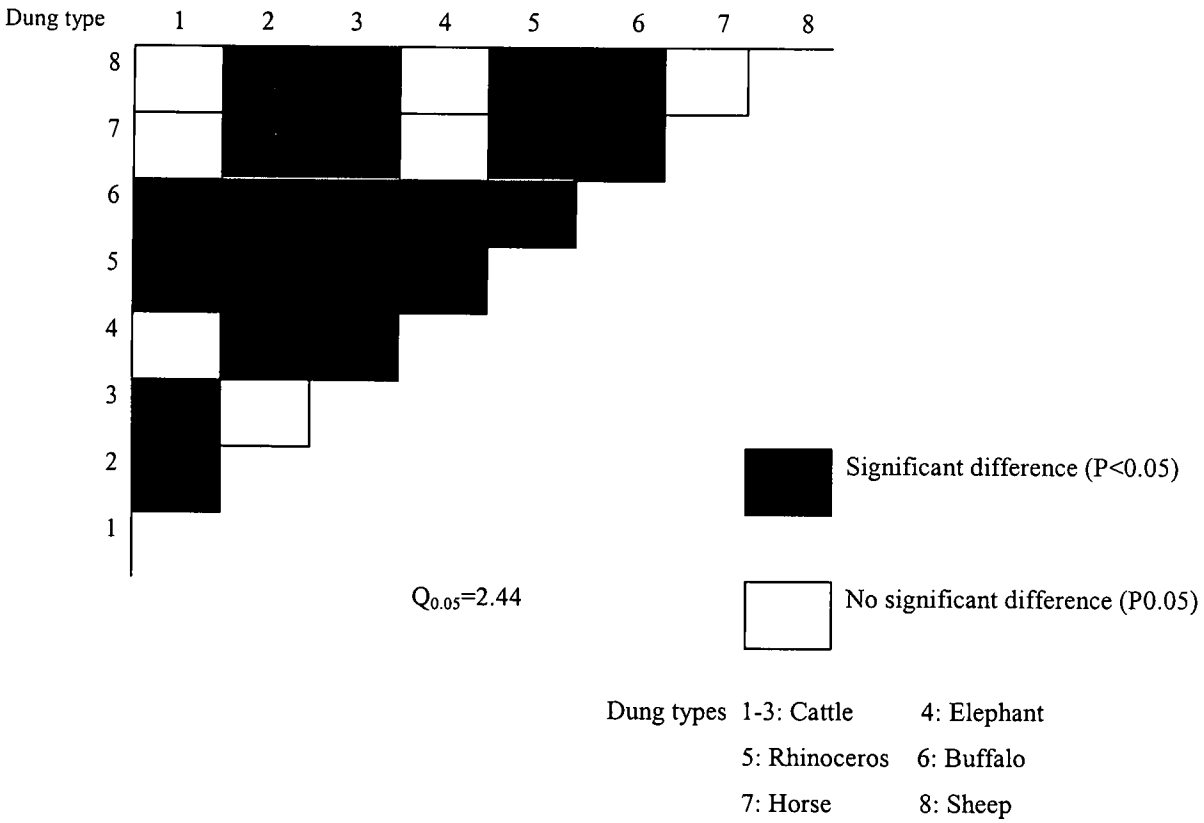


Figure A6.5: A schematic presentation of the significant differences in survival of *Coproica vagans* pupae in different dung types.

Table A6.6: Analysis of variance of survival of *Coproica hirtula* pupae on different dung types.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	989.428571	7	141.346939	2.30345191	0.04151768	2.20743601
Error	2945.42857	48	61.3630952			
Total	3934.85714	55				

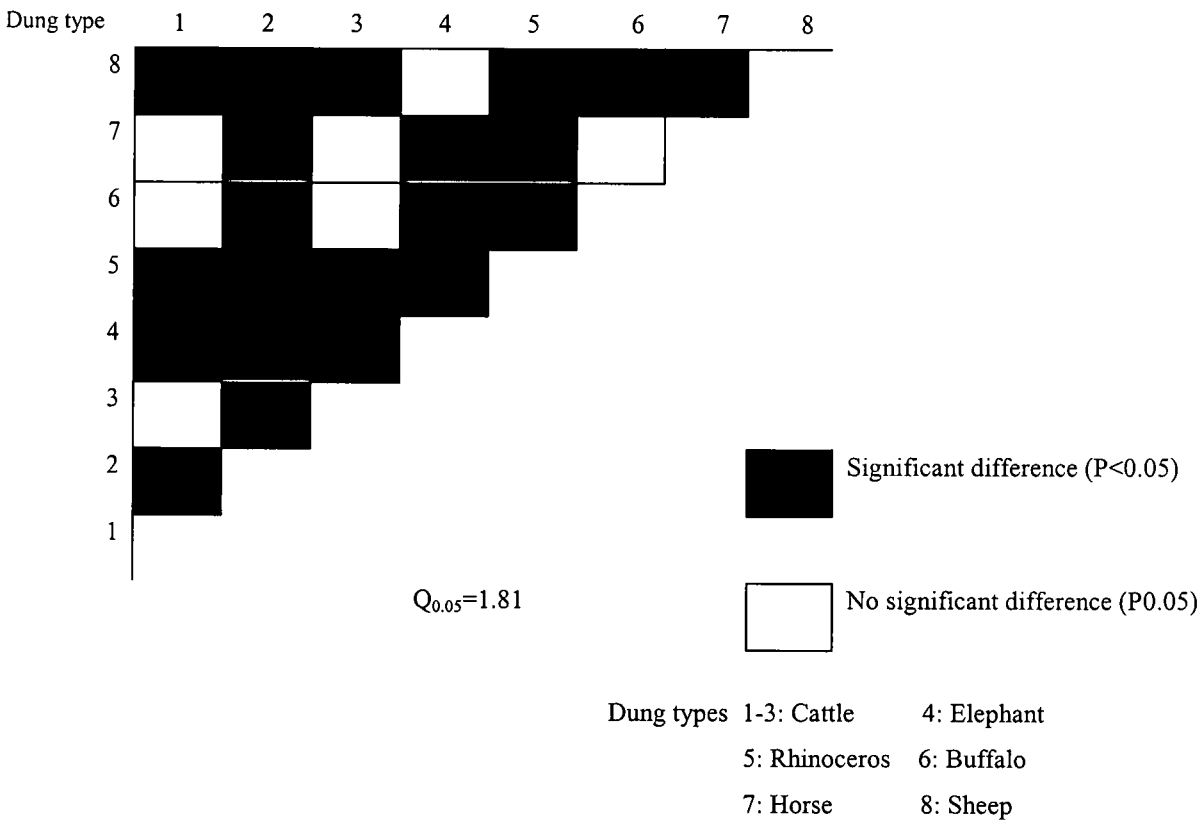


Figure A6.6: A schematic presentation of the significant differences in survival of *Coproica hirtula* pupae in different dung types.

Table A6.7: Analysis of variance of survival of *Coproica vagans* adults on different dung types.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	989.428571	7	141.346939	2.30345191	0.04151768	2.20743601
Error	2945.42857	48	61.3630952			
Total	3934.85714	55				

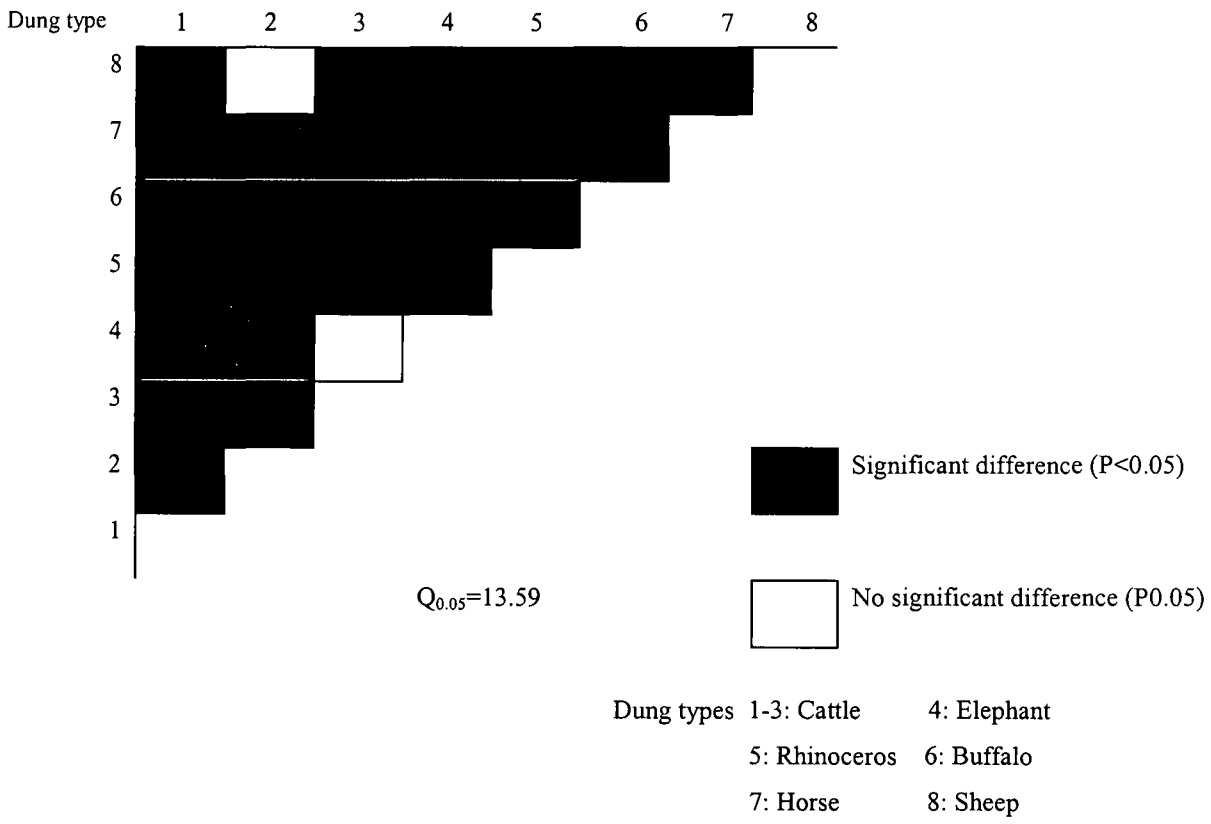


Figure A6.7: A schematic presentation of the significant differences in life expectancy of *Coproica vagans* adults on different dung types.

Table A6.8: Analysis of variance of survival of *Coproica hirtula* adults on different dung types.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	1250.57143	7	178.653061	26.7740538	1.5639E-14	2.20743601
Error	320.285714	72	6.67261905			
Total	1570.85714	79				

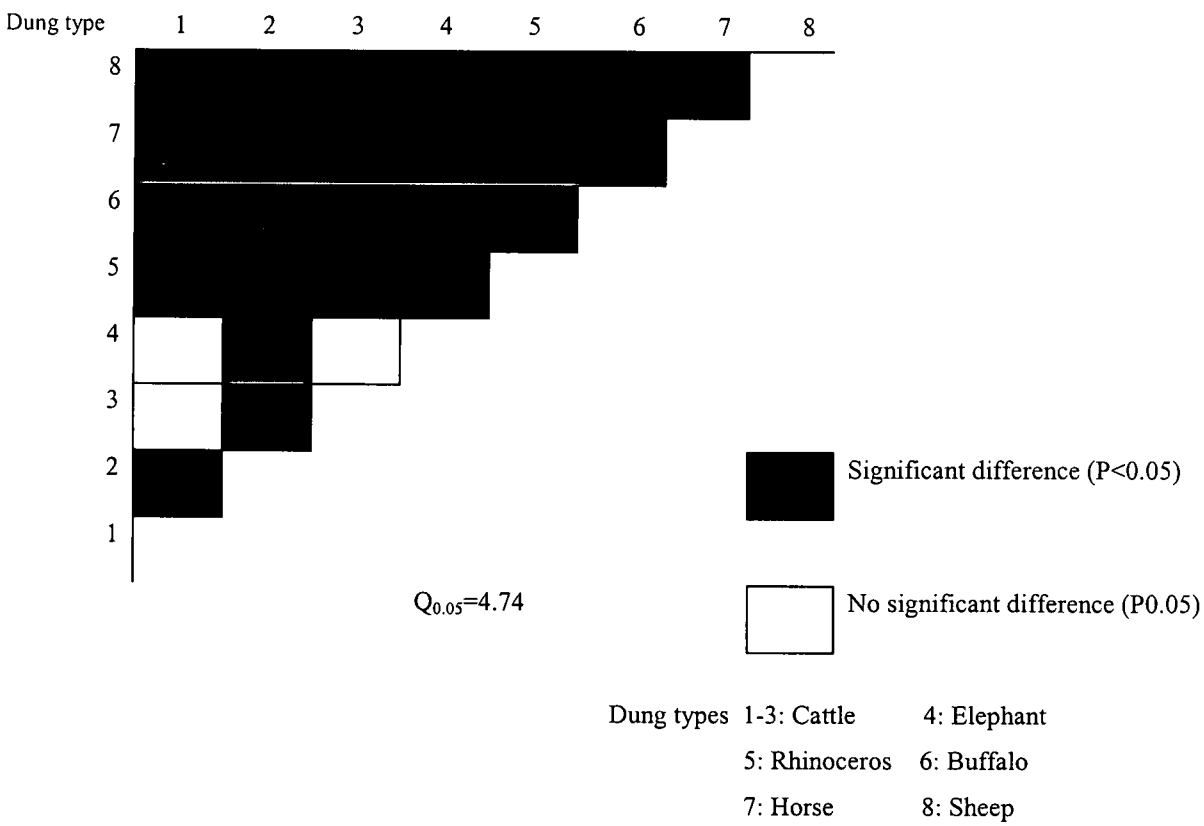


Figure A6.8: A schematic presentation of the significant differences in life expectancy of *Coproica hirtula* adults on different dung types.

Table A 6.9: Results from t-tests (indicated by P-values) in comparing survival between all stages of *Coproica vagans* and *Coproica hirtula* on different dung types.

Dung types	1	2	3	4	5	6	7	8
Eggs	0.016*	0.019*	0.038*	0.040*	0.039*	0.999	0.031*	0.009*
Larvae	0.029*	0.040*	0.042*	0.025*	0.371	0.036*	0.018*	0.033*
Pupae	0.022*	0.030*	0.999	0.013*	0.039*	0.036*	0.021*	0.018*
Adults	0.023*	0.016*	0.999	0.999	0.999	0.011*	0.022*	0.017*

(* indicate significant difference [P<0.05])

Dung types 1-3: Cattle 4: Elephant
5: Rhinoceros 6: Buffalo
7: Horse 8: Sheep

CHAPTER 7

INFLUENCE OF VARIOUS INVERTEBRATE SPECIES ON REPRODUCTION AND SURVIVAL OF SPHAEROCERIDAE AT FEEDLOTS

7.1 INTRODUCTION

Numerous Diptera species usually feed on and develop in manure of domestic animals that were congregated artificially by man at dairies, poultry houses or feedlots (Legner & Olten, 1970). These flies are, prior to pupation, often subjected to predation or parasitism by a number of predatory arthropods. They also mentioned that for a number of coprophagous Diptera, it is the accumulation of manure into piles, rather than its composition, which usually attracts the females (Legner & Olten, 1970).

Dung breeding flies are pests of livestock in various parts of the world. In the past years various authors, *e.g.* Sanders & Dobson (1969) and Blume *et al.* (1970) gave attention to the relationship and interactions between immature stages of dung inhabiting flies and other organisms that share the same habitat. Garry & Wingo (1971), in their investigations on the ecology of the face fly, *M. autumnalis*, showed that natural enemies, such as coleopterous predators and hymenopterous parasites, have some role to play in reducing the number of flies that survive from egg through to adult stage. Axtell (1963) studied the effect of a mite, *Macrocheles muscaedomesticae* (Scopoli) on house flies, while others such as Legner & Brydon (1966) studied the effect of six hymenopterous parasites on the pupae of *Fannia femoralis* (Stein) and *Ophyra leucostoma* (Wiedemann) in California. In Australia, intensive research was carried out on the biology and control of the Australian bush fly, *M. vetustissima*, a widespread and irritating pest of man (Muirhead-Thomson, 1988). This project was extended to South Africa and Spain in search of exotic dung beetles or allied controlling agents to deal with the bush fly (Muirhead-Thomson, 1988).

The aim of this study was to determine the influence of invertebrates present in cattle dung on the development and survival of Sphaeroceridae. Such information might prove useful when a biological control program against Sphaeroceridae in the feedlots is considered or developed.

7.2 MATERIAL AND METHODS

During this study six different invertebrate species were used. These included two endocoprophagous dung beetles, *Aphodius pseudolividus* Balthasar and *Harmogaster strydomi* Endrödi, a staphlinid beetle, *Philonthus caffer* (Boheman) and two fly species, *Coboldia fuscipes* (Meigen) (Scatopsidae) and *M. xanthomelas* Wiedemann (Muscidae). Unidentified mite species from Blokhuis feedlot were also used. Identification of the mites was almost impossible as more than 100 genera were present in each sample (Camerik, pers. comm.). Due to the costs involved in identification, it was decided to use the mites indiscriminately and refer to them as mites in general, irrespective whether they were predacious or not. If the results were to be positive, further identification of the mites would be considered at a later stage.

The two dung beetle species *A. pseudolividus* and *H. strydomi* were collected at Hebron, a farm 20 km west of Bloemfontein (29°06'S ; 26°01'E). Dung pats were collected and brought to the laboratory where the dung beetles were removed. Staphylinidae were collected at Blokhuis feedlot near Harrismith (28°15'S ; 29°07'E). The dung was collected in plastic containers and brought to the laboratory where the Staphylinidae were retrieved. The two fly species, as well as the mites, were collected from dung collected at Blokhuis feedlot and Hebron. The two Sphaeroceridae species *C. vagans* and *C. hirtula* used in the study were taken from established laboratory colonies maintained at the Department of Zoology and Entomology at the University of the Orange Free State.

In studying the interspecific competition between sphaerocerid species and other insect species, the same experimental procedures were followed throughout. Each of the seven experiments was repeated three times. Soft moist sand was placed in plastic containers (12 x 7 x 6 cm) and covered the bottom. Small 100g pats made of fresh, one-day-old moist dung collected at Hebron were placed individually into each container. Equal numbers of *C. vagans* and *C. hirtula* adults (100 of each) were transferred to the prepared containers. This was done because the two species co-existed at the feedlot and an attempt was made to simulate feedlot conditions in the laboratory as closely as possible. Furthermore, because the influence of the six insect species and mites were tested on Sphaeroceridae in general, it was decided not to separate the two Sphaeroceridae species during this experiment. These 200 adult Sphaeroceridae flies (50 males and 50 females of each species) were put into each container and allowed to oviposit on the dung. After three days the adults were removed to prevent any confusion between the parent generation and the progeny (F1). Counting of eggs oviposited by the Sphaeroceridae without physically moving the dung pats was impossible because of the size of the eggs and also because of the numerous cracks and crevices in and underneath the dung pats. The eggs that were oviposited by the flies and beetles were therefore left undisturbed and allowed to hatch. Initially this methodology caused some concern, because of the danger in assuming that equal number of flies produced equal number for eggs. However, for each individual experiment, the control repetition was repeated three times, as mentioned before, and this proved that the number of Sphaeroceridae flies that emerged from each control never deviated by more than 20% from one another. This clearly indicated that this experimental procedure was accurate enough to use if a 20% deviation in accuracy and precision would be accepted. Larvae were also allowed to develop to adulthood without any disturbance. The containers were covered with gauze to prevent the insects from escaping, but also to facilitate ventilation. With each of these seven experiments a control treatment containing only the 200 Sphaeroceridae adult flies was included. This control treatment was prepared and maintained in the same way as the rest of the treatments.

7.2.1 Coleoptera

Three different Coleoptera species were used, two endocoprophagous dung beetle species (*A. pseudolividus* and *H. strydomi*) and one staphylinid beetle. The staphylinid beetles *P. caffer* and *Philonthus ventralis* (Gravenhorst) were present at the feedlot in the drier dung underneath the peripheral fences around the camps. *Philonthus caffer* was used since it was more abundant at the feedlot than *P. ventralis*. The genus *Philonthus* is well documented as predators of dung breeding flies (Roth *et al.*, 1983). Three different experiments were conducted, two in which the dung beetles were used and one for the staphylinid. Each experiment consisted of six different treatments containing 10, 20, 30, 40 or 50 adult beetles respectively which were placed in individually prepared containers, as well as one control container without any beetles. After all the flies had emerged and were counted, the dung was scrutinized and the number of dung beetle and staphylinid larvae present was also counted. No dung beetle pupae had yet been formed at this stage.

7.2.2 Diptera

Each experiment consisted of five different treatments for each fly species. For *C. fuscipes*, the series consisted of 50, 100, 200 and 300 flies in each container and for *M. xanthomelas* 20, 30, 40 and 50 flies were used. The reason why a maximum of 300 Scatopsidae individuals were used and only 50 Muscidae, was because the latter flies were larger. A larger number of muscids, for example 300 individuals, would have been too many for the small sized pats and the size of the containers used. All flies were removed from the containers after five days.

7.2.3 Acari

This experiment consisted of a set of four treatments. The first treatment, with a low number of mites, contained approximately 22 mites/cm^2. The second treatment, a moderate or medium number, contained approximately 32 mites/cm^2 and the third treatment, a high number, contained approximately 48 mites/cm^2. A fourth treatment, the control, was without any mites. Two hundred Sphaeroceridae flies (50 males and 50 females of each species) were put into each container and were removed three days later, after oviposition had taken place.

All the containers of the different experiments were kept in temperature controlled incubators set at 24 ± 1°C and were kept moist by adding distilled water on a daily basis to prevent desiccation of the dung, larvae and pupae. Observations were made daily, and all the flies that emerged were removed and counted. Each experiment lasted approximately three weeks, until no more adult flies had emerged.

7.3 RESULTS AND DISCUSSION

7.3.1 Coleoptera

7.3.1.1 Scarabaeidae

Variations were observed in the number of flies that were produced between the different treatments where *A. pseudolividus* was present (Fig. 7.1). In the *A. pseudolividus* experiment, significantly more flies emerged from the dung pats containing 10, 20, 30 and 40 beetles than from the pats with 50 beetles, although emergence figures here were still relatively high (Fig. 7.1). With 50 *A. pseudolividus* adult dung beetles and 92 dung beetle larvae present in only 100 grams of dung, an average of 676 ± 75.2 sphaerocerids still emerged from the same dung pat. This

phenomenon also occurred at the 40 beetles per pat replicate where a 100 gram dung pat, containing 40 adult dung beetles and 65 beetle larvae, still produced an average of 1323 ± 182.5 sphaerocerids (Fig. 7.1). The other three replicates (10, 20 and 30 beetles per pat) produced very few dung beetle larvae, and more than 1300 flies emerged from each of these pats, the numbers increasing with decreasing dung beetle numbers (Fig. 7.1).

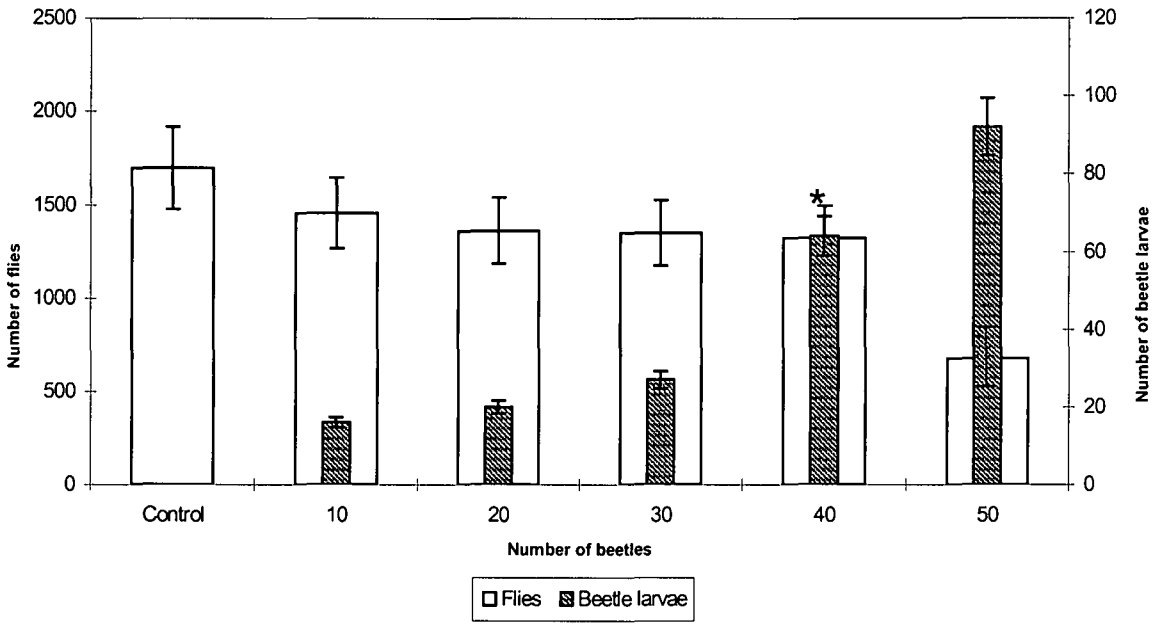


Figure 7.1: The average numbers of adult Sphaeroceridae and *Aphodius pseudolividus* larvae that developed in the same dung pat (* ± SD for the flies).

With analysis of variance ($F_{66;5}$=2.52), significant differences ($P<0.05$) were shown in the number of Sphaeroceridae flies that developed from different cattle dung pats containing different densities of *A. pseudolividus* adults (Table A7.1). Tukey's test ($Q_{0.05}$=1.41) indicated that the number of flies that emerged from the control treatment was significantly higher compared to the rest of the treatments. The number of flies that emerged from the 50 beetles per pat replicate were significantly lower than all the other treatments, while 10 beetles per pat also differed significantly from the rest (Fig. A7.1).

No significant differences were shown to exist between treatments containing 20, 30 and 40 beetles per pat.

All dung pats contained dung beetle larvae except the control (Fig. 7.1) A gradual increase in the number of dung beetle larvae occurred with increases in the number of *A. pseudolividus* beetles per pat. At 50 beetles per pat, more than 90 *A. pseudolividus* larvae were found in some pats (Fig. 7.1). The three treatments with 10 to 30 beetles per pat had less than 30 dung beetle larvae in each 100 gram pat (Fig. 7.1).

Significant differences ($P<0.05$) in the number of *A. pseudolividus* larvae per pat were shown to exist with analysis of variance ($F_{54;5}=5.75$) (Table A7.2). With a Tukey's test ($Q_{0.05}=2.41$), it was shown that the number of *A. pseudolividus* larvae present in the 50 beetles per pat treatment was significantly higher compared to all the other values (Fig A7.2). The rest of the values all differed significantly from one another (Fig. A 7.2).

Similar results were found with *H. strydomi* introduced to the dung pats. On average, more than 1100 Sphaeroceridae flies emerged from the different pats, except at 30 beetles per pat (Fig 7.2). Here, 58 dung beetle larvae were found, and despite their presence and that of adult beetles, an average of 817 ± 42.8 Sphaeroceridae successfully developed to adulthood in the 100 gram dung pat (Fig. 7.2). The increase in Sphaeroceridae numbers at 40 and 50 beetles per pat could be contributed to a decrease in beetle larvae in these dung pats. This decrease in the number of dung beetle larvae could be as a direct result of interspecific competition between the fly larvae and the dung beetle larvae, or intraspecific competition among the dung beetle larvae, causing a decline in their numbers.

Analysis of variance ($F_{66;5}=9.19$) showed that significant differences ($P<0.05$) existed in the number of Sphaeroceridae flies that emerged from dung pats containing different densities of *H. strydomi* adults (Table A7.3). Tukey's test ($Q_{0.05}=5.05$) indicated that the

number of Sphaeroceridae flies that emerged from the pat containing 30 beetles was significantly lower compared to the rest of the treatments (Fig. A7.3). In the same manner, the number of flies that developed at the control pats was significantly higher than the rest of the treatments. However, no significant differences were found in the number of Sphaeroceridae flies that emerged between the 10, 40 and 50 beetles per pat (Fig. A 7.3). The number of Sphaeroceridae that emerged from the 20 beetles per pat treatments was also significantly different from the rest of the replicates in the experiment.

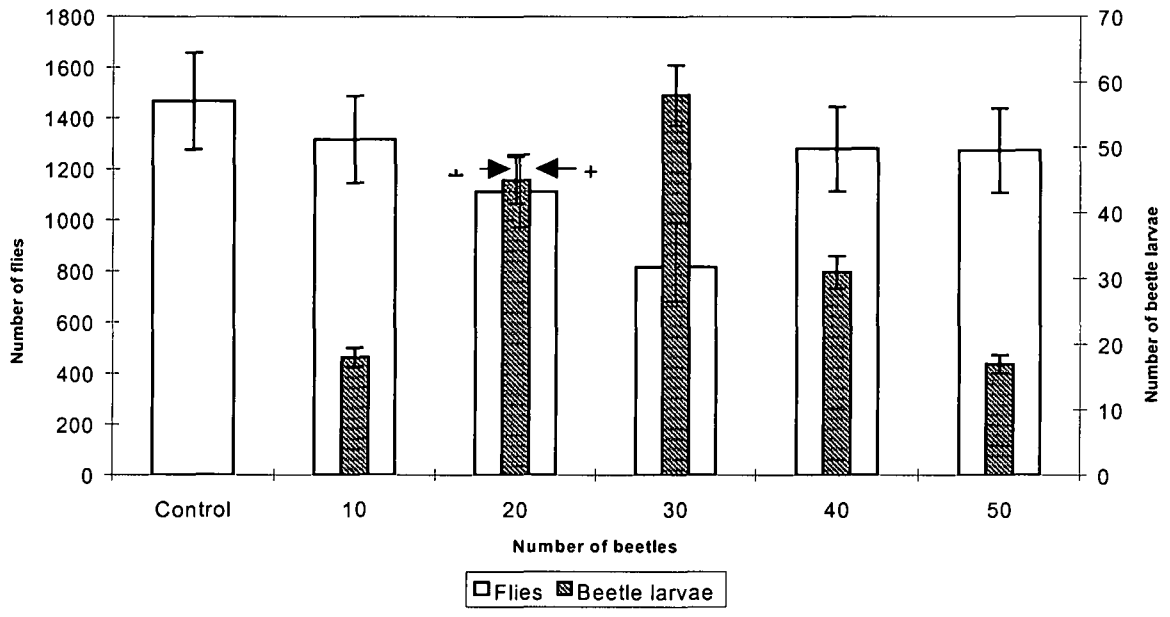


Figure 7.2: The average numbers of adult Sphaeroceridae and *Harmogaster strydomi* larvae that developed in the same dung pat. (* ± SD for flies; + ± SD for beetle larvae).

The number of *H. strydomi* larvae present in the dung varied between 17 and 58 for the different replicates (Fig. 7.2), which clearly indicated the insignificant effect that these dung beetles could exert on Sphaeroceridae. In contrast to what was found with *A. pseudolividus*, the number of *H. strydomi* larvae in the dung showed a decrease at the 40

and 50 beetles per pat treatments (Fig. 7.2). The reason for this is uncertain, but it could be that fewer beetle larvae survived in these dung pats due to intraspecific competition. Analysis of variance ($F_{54;5}$=46.13) showed significant differences ($P<0.05$) in the number of *H. strydomi* larvae present in the dung pats (Table A7.4). Tukey's test ($Q_{0.05}$=21.39) indicated that the number of *H. strydomi* larvae found in the different dung pats differed significantly from one another, except between the 10 and 50 beetles per pat, where no significant differences were found (Fig. A7.4).

Although the exact number of eggs produced by dung beetles in each dung pat is unknown, and even if these do differ, the results still indicate that both endocoprophagous beetles, *A. pseudolividus* and *H. strydomi*, only had a minimal influence on the number of flies that emerged from dung pats. The only exceptions were at 50 *A. pseudolividus* beetles per pat and 30 *H. strydomi* beetles per pat where fly emergence dropped to below 50% compared to the control group. Although this drop in adult emergence was significant in both cases, it would still not be sufficient to control Sphaeroceridae effectively at feedlots. Among the *A. pseudolividus* and Sphaeroceridae, interspecific interactions could be seen, because an increase in the number of dung beetles and their larvae caused a decreased in the number of Sphaeroceridae that emerged from the dung pats. In the case of *H. strydomi*, intraspecific interactions among the dung beetle larvae were very obvious, since the number of dung beetle larvae in the dung decreased as the number of adult beetles in the dung increased. Initially it was thought that the number of dung beetles and dung beetle larvae present in dung pats might have a detrimental effect on the number of adult sphaerocerid flies that emerged due to interspecific competition. However, the decrease in the number of flies that emerged from the dung pats were significant in some cases, and this corresponds with findings by several authors who were able to show in a number of studies that fly mortality in cattle dung was greater when scarabaeine dung beetles were present (Blume *et al.*, 1973; Macqueen & Beirne, 1975; Ridsdill-Smith *et al.*, 1986).

According to Macqueen & Beirne (1975) there are only three avenues through which flies can be affected by other insects in the dung, namely competition, parasitism and predation. Aphodiinae are endocoprophagous and the effects of parasitism and predation can therefore be eliminated (Macqueen & Beirne, 1975). This leaves competition for space and nutrition as the only way whereby these dung beetles can influence the sphaerocerid populations in the dung. Apart from this, the seasonal habits of these Scarabaeidae, especially *H. strydomi*, also make it unlikely to affect any Sphaeroceridae populations significantly in the field. This is because the Scarabaeidae reached peak numbers mainly during autumn (Geyser, 1994). This was also the view of Macqueen & Beirne (1975), who mentioned that scarabaeids are most abundant in the Canadian autumn, a time when Sphaeroceridae numbers were declining. Although this was applicable to a specific situation in the Northern Hemisphere, much the same patterns were observed during the current studies. Ridsdill-Smith & Hayles (1990) also found that dung beetles killed a greater proportion of bush flies, *M. vetustissima*, through predation in field pats during summer and spring, partly because beetles were more abundant.

Muirhead-Thomsen (1988) placed the activities of dung inhabiting beetles into two well-defined categories. The first group consisted of true predatory beetles such as staphylinids and histerids and a second group include the dung-moving scarab beetles which do not prey on the fly larvae, but whose activities indirectly have an adverse effect on fly breeding. The two dung beetle species used in these experiments, *A. pseudolividus* and *H. strydomi*, fall within the second category. In both fly studies Muirhead-Thomsen (1988) found that scarab beetles rapidly broke up and disintegrated the cow dung mass, ovipositing eggs on dung fragments which they buried. In the process the effective life of the rapidly-drying cow pat was shortened and further growth of bush fly larvae limited (Muirhead-Thomsen, 1988). He furthermore found that at a high beetle density, a close relationship existed between dung beetle numbers and the mortality of fly larvae. It was calculated that a common Australian dung beetle species

Onthophagus sp. caused approximately 27% mortality in fly larvae (Muirhead-Thomsen, 1988). Muirhead-Thomsen (1988) also showed that certain adverse factors, whether climatic or due to dung beetle activity, which did not necessarily kill fly larvae, could still affect their growth to the extent that the survivors were smaller.

This current study was initiated to determine the influence of dung beetles on the development and survival of Sphaeroceridae. However, it could be that flies also had a negative effect on the production of dung beetle larvae when they were present in the dung in large numbers. This could mean that fly larval activity inside the dung pat was extremely vigorous and caused a continuous disturbance, thereby exerting a negative influence on the oviposition activities of dung beetles or on their larval development. This is in agreement with the view of Ridsdill-Smith *et al.* (1986) who found that interspecific competition between the dung beetle *Onthophagus binodis* Thunberg and the bush fly (*M. vetustissima*) not only caused a reduction of 66% and 68% in the number of bush flies in the field and in the laboratory respectively, but also had an effect on the dung beetles in that the production of brood balls was reduced. They also mentioned that dung beetle activity could result in bush fly egg mortality by causing conditions that lead to desiccation (Ridsdill-Smith *et al.*, 1986). Although bush fly larvae are much larger than those of Sphaeroceridae, the large number of Sphaeroceridae larvae in the dung could have been sufficient to exert the same effect on the dung beetles. Hughes *et al.* (1978) also reported that eggs of the Australian bush fly were adversely affected when dung pats were disturbed by the activity of *Euoniticellus intermedius* (Reiche) (Coleoptera: Scarabaeidae). A high level of *M. vetustissima* mortality occurred in the presence of *Onitis alexis* Klug (Coleoptera: Scarabaeidae) and *O. binodis* in experiments both in the laboratory at a constant temperature of 25°C, and natural fluctuating summer temperatures (Ridsdill-Smith & Hayles, 1990). These authors also observed that when beetles arrived at dung at the time when flies oviposited, fewer fly larvae hatched or survived than when the beetles arrived one day later. The beetles presumably killed the *M. vetustissima* eggs (Ridsdill-Smith & Hayles, 1990).

In the present study, the experiments with the Scarabaeidae beetles were done in dung collected at the farm Hebron (Bainsvlei), which was not a feedlot and therefore the composition of the dung was different. However, despite this precaution, the effect that the beetles had on the development and survival of the Sphaeroceridae was not enough to control the fly population completely. A further and more likely explanation why Scarabaeidae beetles would be unable to influence any sphaerocerid populations at the feedlot is their inability to survive in feedlot dung (Geyser, 1994).

7.3.1.2 Staphylinidae

Flies emerged from all dung pats in large numbers. Between 1450 and 2000 flies emerged from each of the dung pats, irrespective of the number of Staphylinidae present in the dung (Fig. 7.3). The number of flies that emerged from dung pats, in which 10 staphylinids were placed, was just as high as in the control where no rove beetles were present. At 50 beetles per pat, an average of 1505 ± 203.2 Sphaeroceridae emerged, compared to the control where 1991 ± 263.9 sphaerocerids successfully developed (Fig. 7.3). However, analysis of variance ($F_{54;5}$=4.91) showed significant differences ($P<0.05$) in the number of Sphaeroceridae flies that emerged from dung pats in which staphylinid beetles were present in different numbers (Table A7.5). Tukey's test ($Q_{0.05}$=3.15) furthermore indicated that the number of sphaerocerid flies that emerged from dung pats with 20 and 40 beetles per pat differed significantly from each other and also from the rest of the treatments. Tukey's test also showed that no significant differences existed between the control and 10 beetles per pat or between 30 and 50 beetles per pat (Fig. A7.5).

The number of Staphylinidae larvae that was found in the same dung pats as the flies was extremely low, and only between 1 and 5 were found (Fig. 7.3). However, analysis of variance ($F_{42;5}$=3.36) still showed significant differences ($P<0.05$) in the number of staphylinid beetle larvae present in the dung (Table A7.6). Tukey's test ($Q_{0.05}$=1.08) was

used to indicate that the number of larvae present in dung with a density of 40 staphylinids beetles per pat was significantly higher compared to the rest of the treatments (Fig. A7.6). The number of larvae at 10 beetles per pat was also significantly lower than the rest (Fig. A7.6). No significant differences could be found between the 30 and 50 beetles per pat treatments (Fig. A7.6).

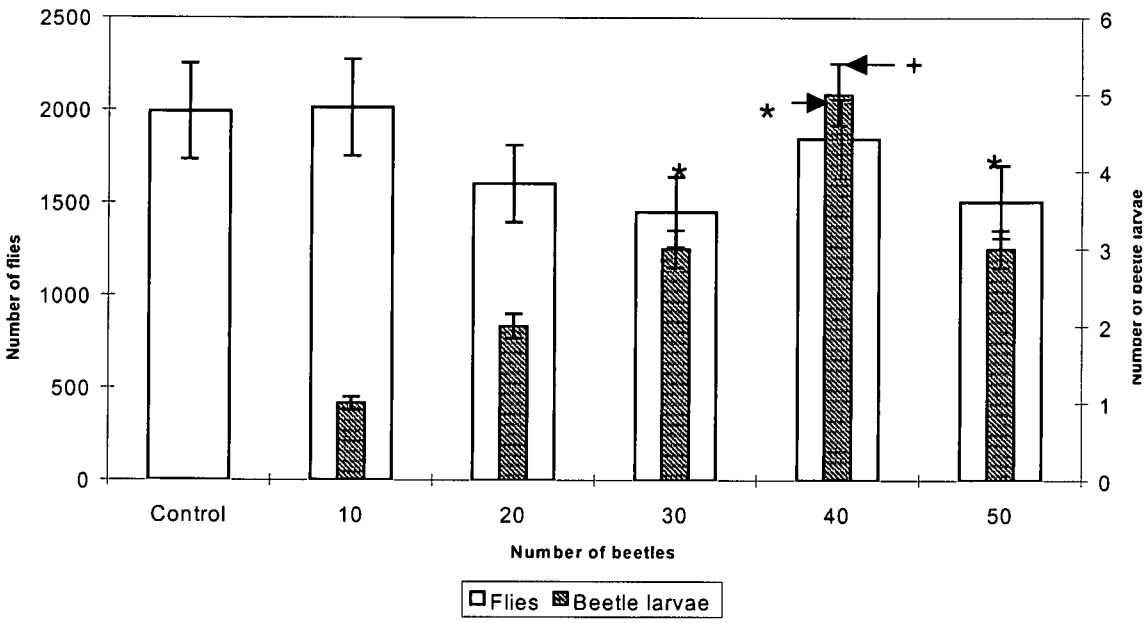


Figure 7.3: The average numbers of adult Sphaeroceridae and *Philonthus caffer* larvae that developed in the same dung pat (* ± SD for flies; + ± SD for beetle larvae).

As the number of rove beetles per pat increased, the number of their larvae also increased. However, at 50 beetles per pat, the number of larvae decreased and was shown to be significantly lower compared to 40 beetles per pat (Fig. A7.6). This could indicate that intraspecific competition existed among the Staphylinidae larvae. Interspecific interactions between the fly larvae and rove beetles were also shown, except at 40 beetles per pat, since the number of flies that emerged decreased compared to the control when the number of staphylinids were increased (Fig. 7.3). It seemed that

at 40 beetles per pat, interspecific competition among the flies and beetle larvae weakened, although the reason for this still remains unclear.

These results furthermore showed that the effect of *P. caffer* adults and their larvae on the production and emergence of sphaerocerid flies were not enough to suppress fly development significantly. A reduction of approximately 25% in the number of Sphaeroceridae that emerged from the dung pats was the maximum success rate that could be achieved through the use of rove beetles. Furthermore it seemed as if staphylinids could not survive optimally in fresh wet dung, because many died within the first few days of the experiment. The few staphylinid larvae that were found in the dung during the experiment appeared very small and weak, and most died during the experiment. Closer observations at Blokhuis feedlot also showed that staphylinids at the feedlot preferred drier, older dung where they formed a network of tunnels in the dung. They were absent inside the camps where dung was frequently very wet and much fresher. Furthermore, trampling by the cattle inside the camps might also make it impossible for staphylinids with ground-living activities to survive in feedlot dung.

In contrast to the above-mentioned, various other studies that involved biological control of flies with Staphylinidae, proved to be successful. Fincher & Summerlin (1994) were able to show that both adult and larval stages of *Philonthus* sp. prey on immature stages of flies in dung deposits. The staphylinid beetle *Aleochara tristis* (Gravenhorst) was introduced from France into the USA in 1965 in an attempt to control face fly (*M. autumnalis*) (Drea, 1966). The larvae of *A. tristis* are parasitoids of Diptera pupae and adults are voracious predators of fly eggs and young larvae (Drea, 1966). According to Thomas & Morgan (1972), *Sphaeridium scarabaeoides* (Linnaeus) was one of the most important staphylinid predators of the horn fly, *H. irritans,* in Missouri. Macqueen & Beirne (1975) found that *Philonthus cruentatus* Gmelin was the most important predator of the horn fly in British Columbia, where they were voracious predators on fly eggs and newly hatched larvae on the surface of dung pats. Research programs concerned with the

biting fly *Haematobia* sp. in South Africa, which mainly breeds in buffalo dung, have shown that predatory staphylinid and histerid beetles caused a significant mortality among immature stages of fly larvae because large numbers of staphylinid beetles had been feeding on these larvae (Muirhead-Thomsen, 1988). Others such as a tropical rove beetle, *Leistotrophus* sp., is a specialized obligate predator of adult Diptera and can be located on vertebrate dung and carrion, where they wait to ambush incoming flies drawn to these materials (Forsyth & Alcock, 1990). Valiela (1974) stated that staphylinid beetles are able to use the ever-present network of burrows created by burrowing dung beetles to reach and prey upon fly larvae that sought protection inside the droppings.

The larvae of flies associated with dung often show very fast growth rates relative to predator insects and therefore the outcome of predator-prey relationships often depends on the relative size of both prey and predator (Valiela, 1974). The faster development rates of Sphaeroceridae in comparison with staphylinid dung beetle larvae could also be one of the reasons why Staphylindae did not have a serious impact on flies in these laboratory studies. Valiela (1974) also stated that *P. cruentatus* was one of the most numerous and active of the staphylinid beetles found in a dung community. However, it was incapable of killing fly larvae over six mm long, although attacks could have taken place, while invertebrates that were too small (under 0.5 mm in length) were overlooked by *Philonthus* sp. (Valiela, 1974). Sphaeroceridae larvae therefore qualify as a food resource for *Philonthus* sp. on account of their size. In this regard Valiela (1974) found that large staphylinid predators were unable to limit large numbers of prey individuals. In turn, predators were never food-limited in communities of dung invertebrates, because there was more than adequate prey biomass to support the predators present (Valiela, 1974). This phenomenon would be particularly applicable to the feedlot setup where the number of Sphaeroceridae larvae present in the dung would be unlimited to any predators, provided they are able to survive in wet feedlot dung.

7.3.2 Diptera

Results showed that *C. fuscipes* had very little effect on the number of sphaerocerids developing in the dung because the number of sphaerocerid that emerged was very similar (between 2850 and 2950) in all five dung pat treatments (Fig. 7.4). This was supported by analysis of variance ($F_{55;4}$=0.99) which showed no significant differences (P>0.05) in the number of Sphaeroceridae flies that emerged from the different dung pats (Table A7.7 & Fig. A7.7). However, the number of scatopsids that emerged from the pats decreased from *ca.* 500 to 150 as the number of Scatopsidae that was originally placed onto the dung pats per dung pat increased (Fig. 7.4).

The reason for this drop in the number of Scatopsidae is unknown, but it could be that due to interspecific interactions, the Sphaeroceridae larvae had a negative impact on the Scatopsidae, and not vice versa as was initially thought, or because of an over-exploitation of a limited resource as the number of flies increased. This could also be attributed to interspecific interactions between the Scatopsidae larvae that caused their own numbers to decrease.

With analysis of variance ($F_{45;4}$=46.13) significant differences (P<0.05) in the number of Scatopsidae flies that emerged from the dung pats were shown (Table A7.8). Tukey's test ($Q_{0.05}$=25.63) showed that significantly lower numbers of Scatopsidae emerged from 50 flies per pat compared to all other treatments, while significantly higher numbers emerged from 50 flies per pat (Fig. A7.8). Significant differences in the number of Scatopsidae flies were also shown between the 100 and 200 flies per pat (Fig A7.8).

The number of *M. xanthomelas* flies that emerged from the small experimental pats was generally very low in comparison with the Sphaeroceridae (Fig. 7.5). From the dung pats with 20 - 50 muscids per pat, only between 4 and 12 adult *M. xanthomelas* flies emerged. However, with analysis of variance ($F_{35;4}$=5.75) significant differences

($P<0.05$) were shown in the number of *M. xanthomelas* flies that developed from dung pats where they were present in different densities (Table A7.10). Tukey's test ($Q_{0.05}=2.98$) indicated that all values between 20 and 50 flies per pat differed significantly from one another (Fig. A7.10).

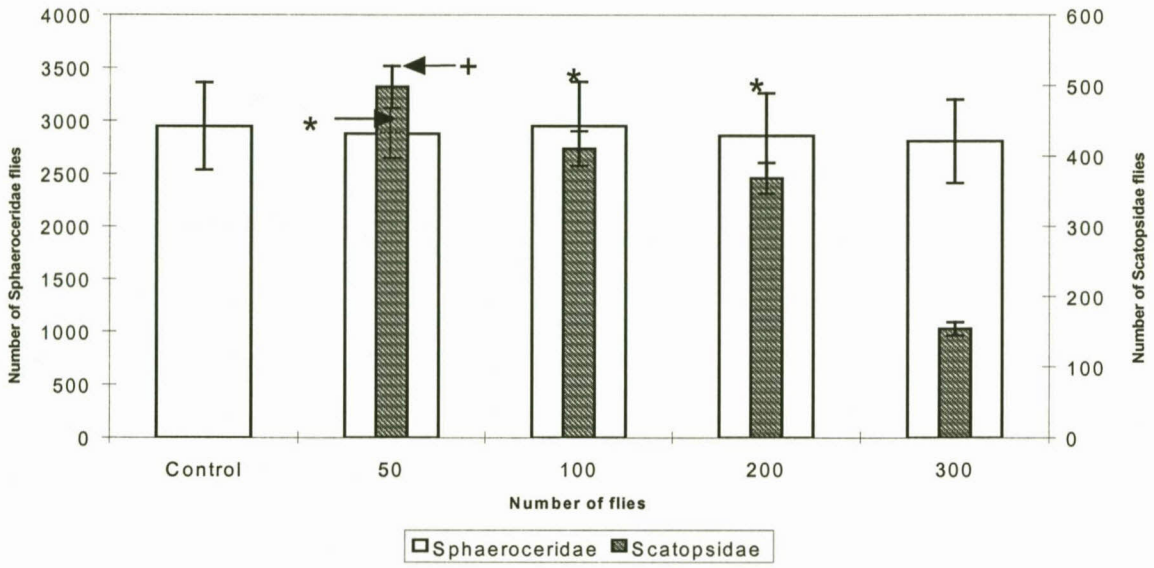


Figure 7.4: The average number of Sphaeroceridae and *Coboldia fuscipes* flies that emerged from dung pats (* ± SD for the Sphaeroceridae flies; + ± SD for Scatopsidae flies).

Musca xanthomelas also had very little effect on sphaerocerids, and the number of Sphaeroceridae that emerged from dung pats in the different treatments were between 900 and 1200. The average of 1121 ± 171.1 sphaerocerid flies which were recorded from the control pat where *M. xanthomelas* was absent, also fell within this range (Fig. 7.5). However, significant differences ($P<0.05$) in the number of Sphaeroceridae adults that emerged from these dung pats were shown with analysis of variance ($F_{55;4}=6.59$) (Table A7.9). With Tukey's test ($Q_{0.05}=12.08$), it was shown that the number of Sphaeroceridae that emerged from 20 flies per pat was significantly lower compared to the rest of the

treatments (Fig. A7.9). No significant differences in Sphaeroceridae numbers were found between the control and 50 flies per pat or between 30 and 50 flies per pat (Fig. A7.9).

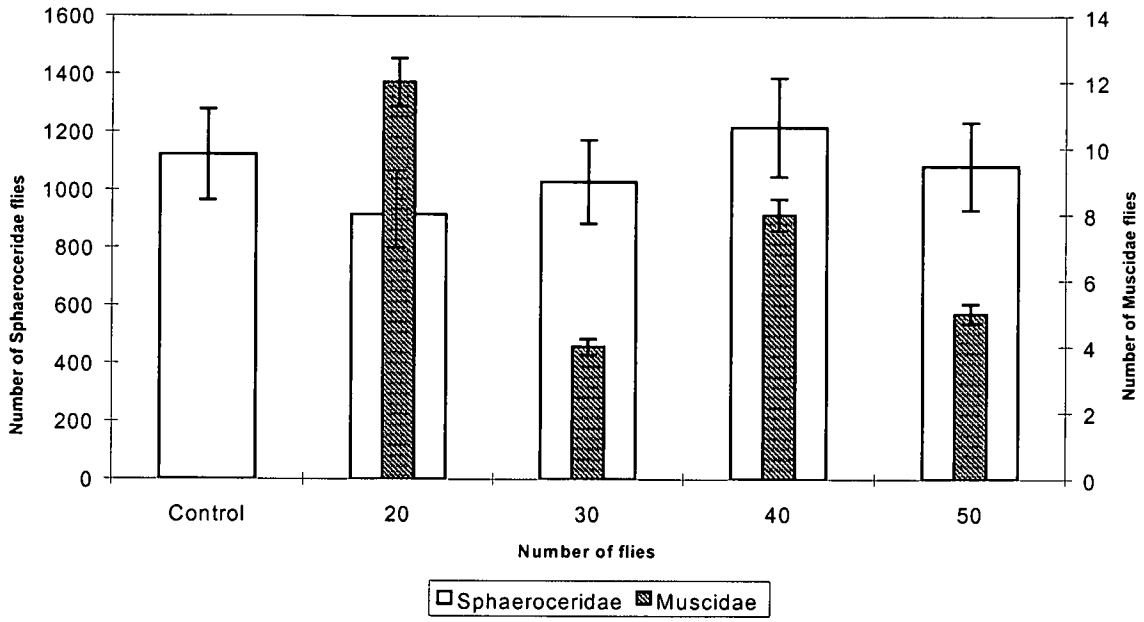


Figure 7.5: The average number of Sphaeroceridae and *Musca xanthomelas* flies that emerged from dung pats.

The first Diptera species that was used as a potential biological control agent in this study was *C. fuscipes* (Scatopsidae). Scatopsidae are generally small, usually black flies, ranging from ca. 0.6 mm to 5.0 mm in size, and the immature stages of only five or six species are known (Cook, 1971). The immature stages of two cosmopolitan species, *Scatopse notata* (Linnaeus) and *C. fuscipes*, occur in a wide diversity of decaying plant and animal material such as cannery and winery waste, as well as bird and mammal excreta (Cook, 1971). Results showed that *C. fuscipes* had no significant influence on the number of Sphaeroceridae adults that emerged from dung pats.

The reason for including *C. fuscipes* in this study was that at one stage they gained access to the sphaerocerid laboratory colonies in particularly large numbers and

destroyed both colonies. It was also discovered that their larvae are predacious. Observations that were made at the feedlot also showed that scatopsids occurred mainly in drier dung in areas underneath the peripheral fences of the feedlot camps. The scatopsid flies that once infested the sphaerocerid laboratory colonies survived on dry dung for up to 24 days. This could explain the poor scatopsid survival in wet feedlot dung. It therefore seems as if Scatopsidae was also not a viable biological control agent, despite of its predacious larvae.

Large numbers of coprophagous Diptera were reared from exposed dung pats under natural field conditions (see Chapter 2), of which Sepsidae, Sphaeroceridae and Muscidae were most abundant. Among the Muscidae that were collected, one species, namely *M. xanthomelas*, was particularly abundant. Subsequently it was decided to include this species in dipteran biological control tests to ascertain whether it would have any influence on Sphaeroceridae in feedlot dung. After the flies were removed from the containers, closer observations showed that very few muscid eggs were laid in the dung, which explains the low emergence figures that were obtained. The reason why so few muscid flies emerged from the 30 flies per pat replicate is unknown. Perhaps it was only a coincidence that female Muscidae did not oviposit many eggs on these particular dung pats or else very few eggs hatched, because conditions were exactly the same for all the different replicates. Most muscoid flies died within the first few days of the experiment. The survival of *M. xanthomelas* in dung from Hebron farm was very good, but in feedlot dung which was used for this particular experiment, survival of maggots and adults were extremely poor. It could be as a result of feedlot dung composition or because the dung was too wet for these muscids. No definite inter- or intraspecific interactions between individuals of *M. xanthomelas* and Sphaeroceridae could be observed during these experiments.

The use of a coprophagous fly species to control another coprophagous fly species through interspecific competition is probably not a good practice. This view was

expressed in several literature references where competition among different fly species was investigated. Poorbaugh *et al.* (1968) regarded competition for food or space among coprophagous Diptera rarely, if ever, an important mortality factor in California. Sands & Hughes (1976) showed that intraspecific competition among bush fly larvae resulted only in a reduction of the size of emerging adults. Valiela (1974) also concluded that competition for food among dung feeders was unlikely to affect mortality of *M. autumnalis*. Competition for food in fly larvae was initially expressed as a reduction in pupal size, and mortality was affected only if exploitation of the resources was severe (Valiela, 1974). Bay *et al.* (1970) showed that face fly larvae require at least 2.0 grams of fresh dung per individual for normal development. No equivalent figures are available for Sphaeroceridae larvae, but in view of their smaller size it would be safe to assume that they should require even less dung than face fly larvae, making interspecific competition with other flies even more unlikely. Macqueen & Beirne (1975) suggested that other mortality factors, *viz.* predation, rather than competition, probably reduced the chances of large coprophagous fly populations developing in dung pats. Moon (1980) stated that competition was a negative, density-dependent interaction among organisms that require a common resource in relative or absolute short supply. He showed that for the face fly, *M. autumnalis*, competition began to affect the flies only when the density of coprophagous larvae exceeded *ca.* 556 larvae per 2 kg pat (Moon, 1980).

7.3.3 Acari

Results showed that the impact of mites on the production of sphaerocerid flies was not as severe as was initially expected. The number of flies that emerged from the three groups of dung pats that were treated with mites was all high (between 500 and 750). The control treatment produced an average of 1053 ± 113 sphaerocerid flies (Fig. 7.6).

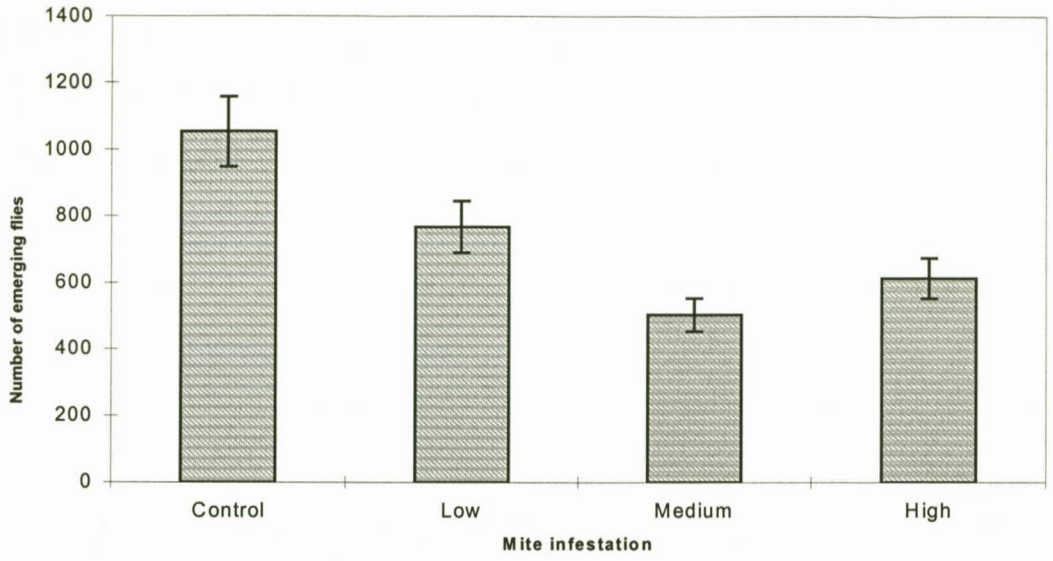


Figure 7.6: The average number of Sphaeroceridae adults that emerged from dung pats infested with mites.

Analysis of variance ($F_{56;3}$=37.23) also showed significant differences ($P<0.05$) in the number of Sphaeroceridae flies that developed on dung infested with different numbers of mites (Table A7.11). Tukey's test ($Q_{0.05}$=18.28) indicated that significantly higher numbers of sphaerocerid flies emerged from the control repetition compared to the low, medium or high mite infestations (Fig. A7.11). The number of sphaerocerid flies that emerged from the different mite infestations all differed significantly from one another.

As mentioned earlier, about 100 genera of mites from different families were present in each sample taken at the feedlot, of which some were definitely predacious species (Camerik, 1993, pers. comm.). Mites were frequently observed in large numbers in the drier dung underneath the peripheral fences at Blokhuis feedlot, and the idea to use them as potential biological control agents for sphaeroceridae flies became apparent after microscopical observations in the laboratory. In laboratory colonies, mites gradually appeared, as the dung became drier. Axtell (1963) also observed the transfer of mites from one colony to another, with the mites attaching themselves to flies or dung beetles and continuing their life cycle in newly established colonies.

Mites in the dung were observed attacking Sphaeroceridae larvae, and on one occasion, three mites were seen attacking one larva. Mites were also seen attacking weak and dying adult flies on the surface of the dung. Results showed that although mites caused a reduction of almost 50% in the number of Sphaeroceridae flies that emerged from the dung, their influence was not strong enough to reduce Sphaeroceridae numbers effectively. At the medium mite density for example, more than 500 flies emerged from a small 100 g dung pat. This is in agreement with the findings from Macqueen & Beirne (1975) who suggested that attacks by dung inhabiting invertebrates on adult flies have very little influence on the fly populations because most flies have already left the pats before many of these dung breeding invertebrates started appearing. Studies in the laboratory showed that in general mites had difficulty in surviving in wet, fresh dung and many had died during the first two days of the experiment. This explains why mites were only found in the drier dung around the feedlot camps, and not inside the wet camps. Rodriques & Wade (1961) also found that substrate differences influenced the rate of predation by mites on house fly eggs under laboratory conditions because the survival of the mites on some substrates was better than on others.

Axtell (1963) re-evaluated the association between the mite *M. muscaedomesticae* and the house fly *M. domestica* and concluded that mites mostly attack eggs and first instar larvae by piercing the chorion or integument and sucking out the content. Valiela (1974) also found that mites, particularly macrochelids and uropodids, fed mainly on fly eggs rather than on larvae. Besides, house fly larvae in the second and third instars were not usually consumed by mites (Axtell, 1963). In general it was found that fly production from manure piles containing mites was significantly less than from piles without mites (Axtell, 1963). He furthermore showed that when the mite *M. muscaedomesticae* was present on calf manure, 61% - 67% fewer house flies, *M. domestica*, survived (Axtell, 1963). Similarly Muirhead-Thomsen (1988) found that the predatory mite *Macrocheles* sp. also had an adverse effect on the Australian bush fly, *M. vetustissima*.

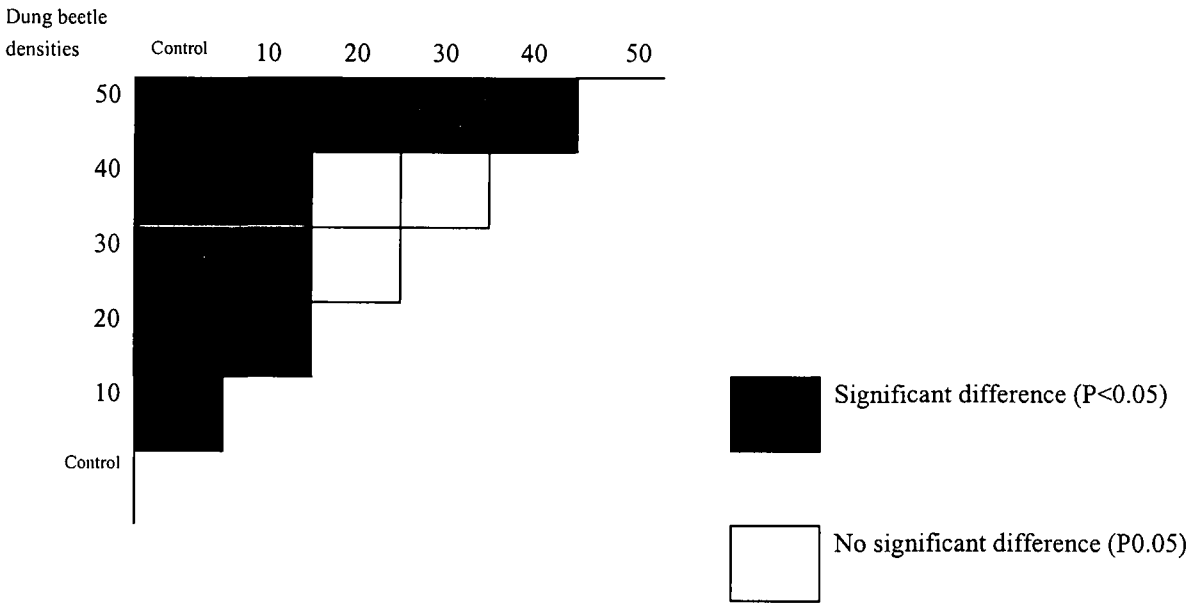
From these experiments it became clear that interactions between immature and adult Sphaeroceridae and other dung breeding invertebrates are very complex. By simply trying to interpret these results in terms of competition or predation would not suffice. Feedlot conditions will complicate these matters even further, and more research is needed before this form of control could be successfully implemented.

7.4 APPENDIX

Table A7.1: Analysis of variance of the number of Sphaeroceridae flies that emerged from dung pats containing different densities of *Aphodius pseudolividus* dung beetles.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	885138.976	5	177027.795	2.51693828	0.04711718	2.47716514
Error	2532044.86	66	70334.5794			
Total	3417183.83	71				



$Q_{0.05}$=1.41

Figure A7.1: A schematic presentation of the significant differences in the number of Sphaeroceridae emerging from dung pats which contained different densities of *Aphodius pseudolividus* dung beetles.

Table A7.2: Analysis of variance of the number of dung beetle larvae present in dung pats containing different densities of *Aphodius pseudolividus* dung beetles.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	710.392857	5	236.797619	5.7538328	0.00410836	3.00878611
Error	987.714286	54	41.1547619			
Total	1698.10714	59				

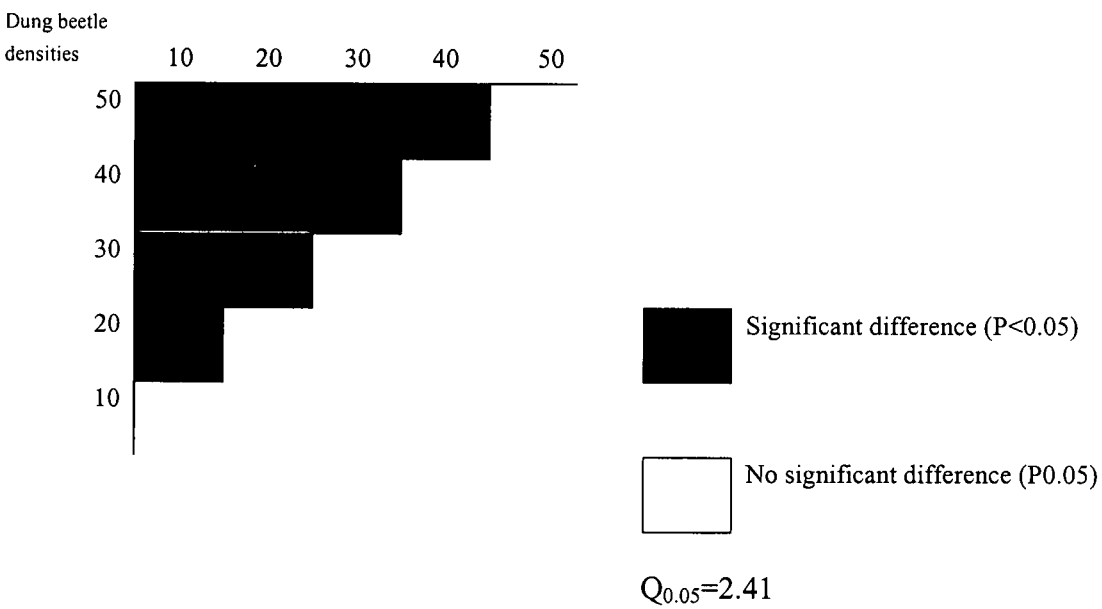
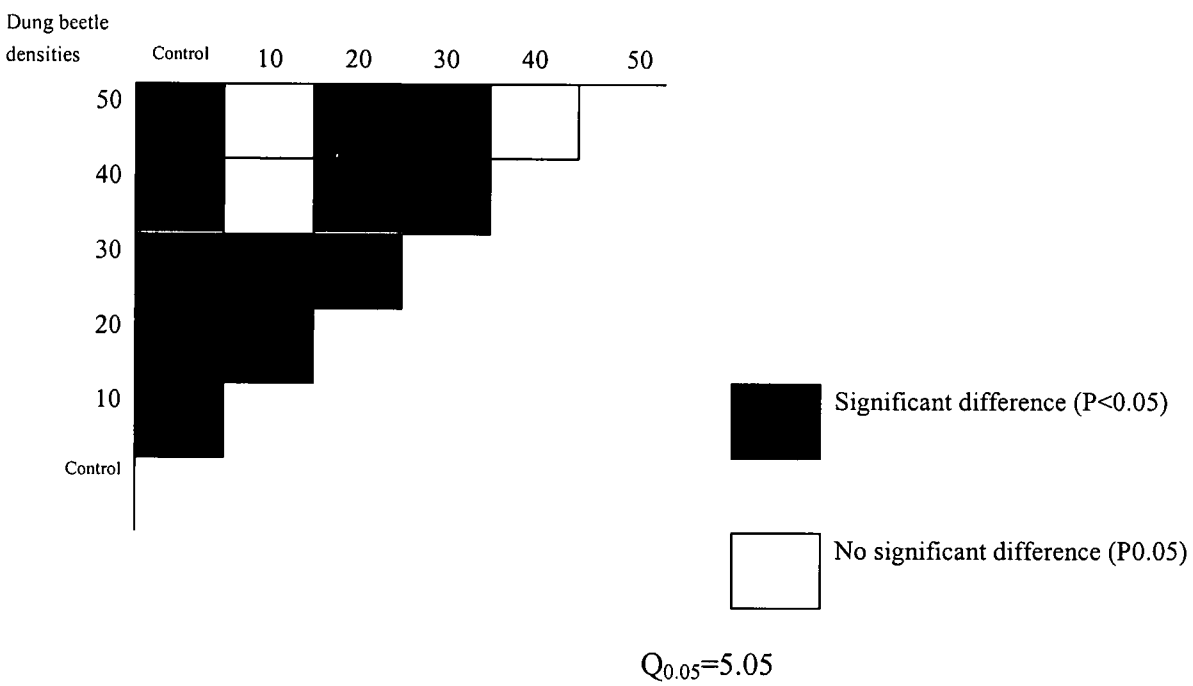


Figure A7.2: A schematic presentation of the significant differences in the number of dung beetle larvae emerging from dung pats which contained different densities of *Aphodius pseudolividus* dung beetles.

Table A7.3: Analysis of variance of the number of Sphaeroceridae flies that emerged from dung pats containing different densities of *Harmogaster strydomi* dung beetles.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	963947.262	5	192789.452	9.18534827	1.0574E-05	2.47716514
Error	755596.857	66	20988.8016			
Total	1719544.12	71				



$Q_{0.05}$=5.05

Figure A7.3: A schematic presentation of the significant differences in the number of Sphaeroceridae emerging from dung pats which contained different densities of *Harmogaster strydomi* dung beetles.

Table A7.4: Analysis of variance of the number of dung beetle larvae present in dung pats containing different densities of *Harmogaster strydomi* dung beetles.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	438321.571	5	146107.19	46.1285344	4.0678E-10	3.00878611
Error	76017.4286	54	3167.39286			
Total	514339	59				

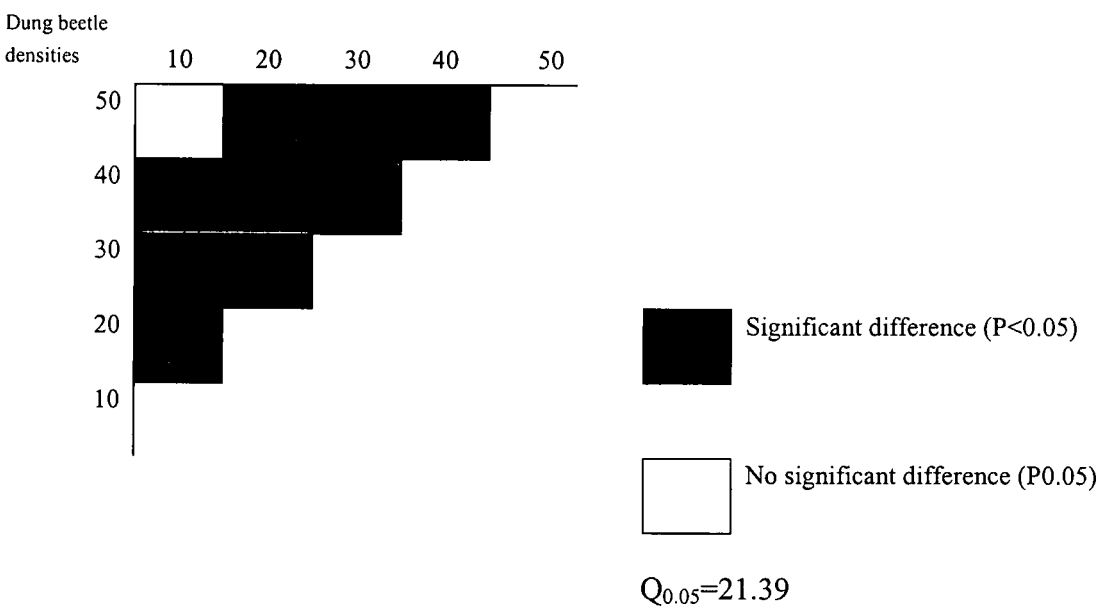
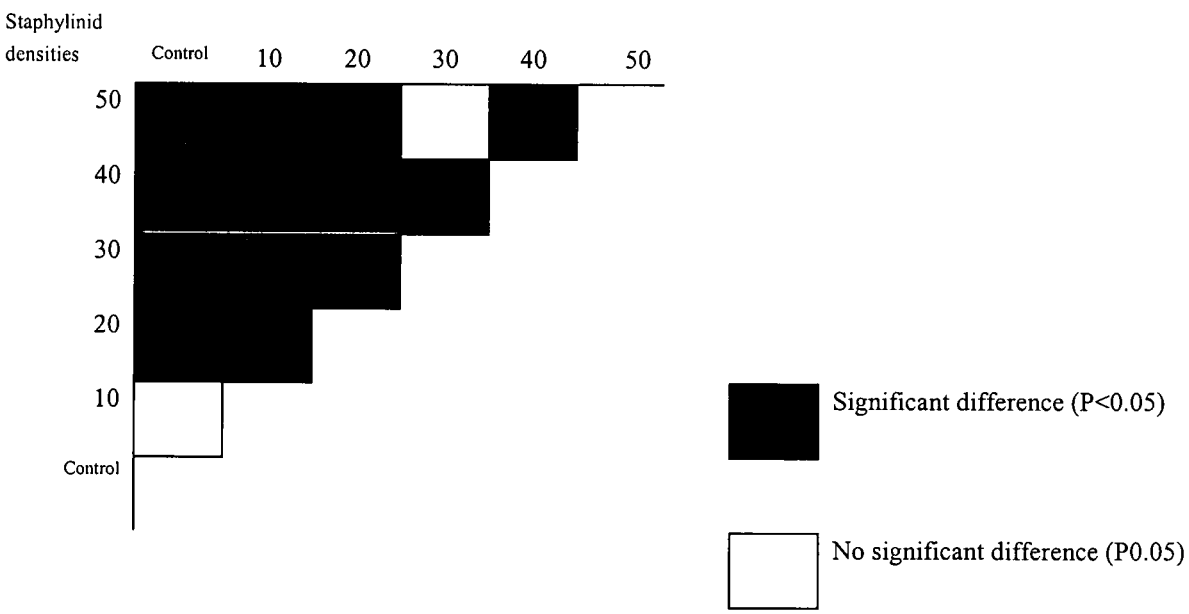


Figure A7.4: A schematic presentation of the significant differences in the number of dung beetle larvae emerging from dung pats which contained different densities of *Harmogaster strydomi* dung beetles.

Table A7.5: Analysis of variance of the number of Sphaeroceridae flies that emerged from dung pats containing different densities of *Philonthus caffer* staphylinid beetles.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	870454.119	5	174090.824	4.90768082	0.00158753	2.47716514
Error	1277032.86	54	35473.1349			
Total	2147486.98	59				



$Q_{0.05}$=3.15

Figure A7.5: A schematic presentation of the significant differences in the number of Sphaeroceridae emerging from dung pats which contained different densities of *Philonthus caffer* staphylinid beetles

Table A7.6: Analysis of variance of the number of staphylinid larvae present in dung pats containing different densities of *Philonthus caffer* staphylinid beetles.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	68.8571429	5	17.2142857	3.35966543	0.02187736	2.68963163
Error	153.714286	42	5.12380952			
Total	222.571429	47				

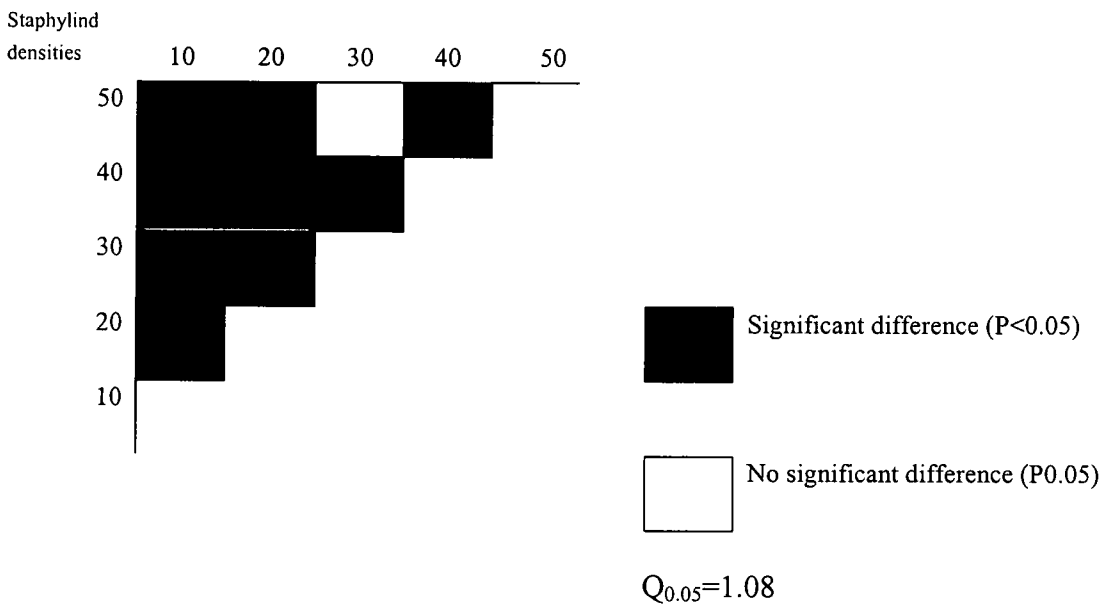


Figure A7.6: A schematic presentation of the significant differences in the number of Staphylinidae larvae emerging from dung pats which contained different densities of *Philonthus caffer* staphylinid beetles.

Table A7.7: Analysis of variance of the number of Sphaeroceridae flies that emerged from dung pats containing different densities of *Coboldia fuscipes* flies.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	177037.543	4	44259.3857	0.98726426	0.42945827	2.68963163
Error	1344910	55	44830.3333			
Total	1521947.54	59				

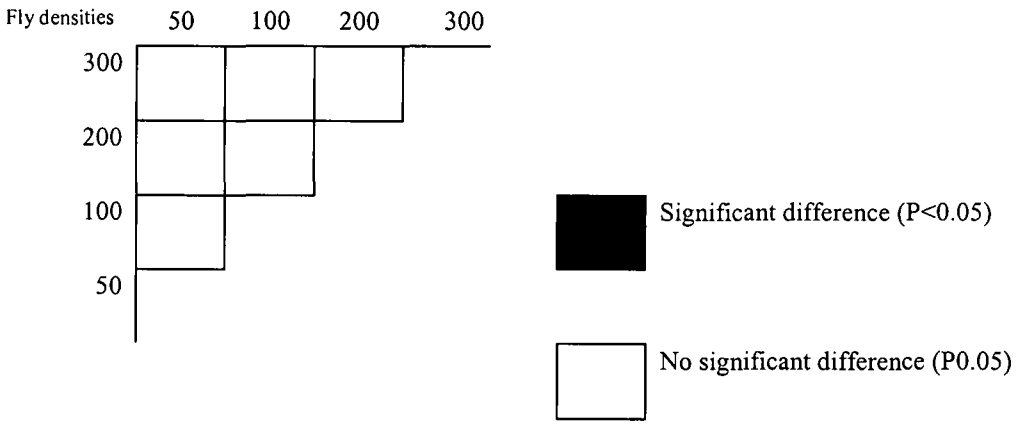


Figure A7.7: A schematic presentation of the significant differences in the number of Sphaeroceridae flies that emerged from dung pats containing different densities of *Coboldia fuscipes*.

Table A7.8: Analysis of variance of the number of Scatopsidae flies that emerged from dung pats containing different densities of *Coboldia fuscipes* flies.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	438321.571	4	146107.19	46.1285344	4.0678E-10	3.00878611
Error	76017.4286	45	3167.39286			
Total	514339	49				

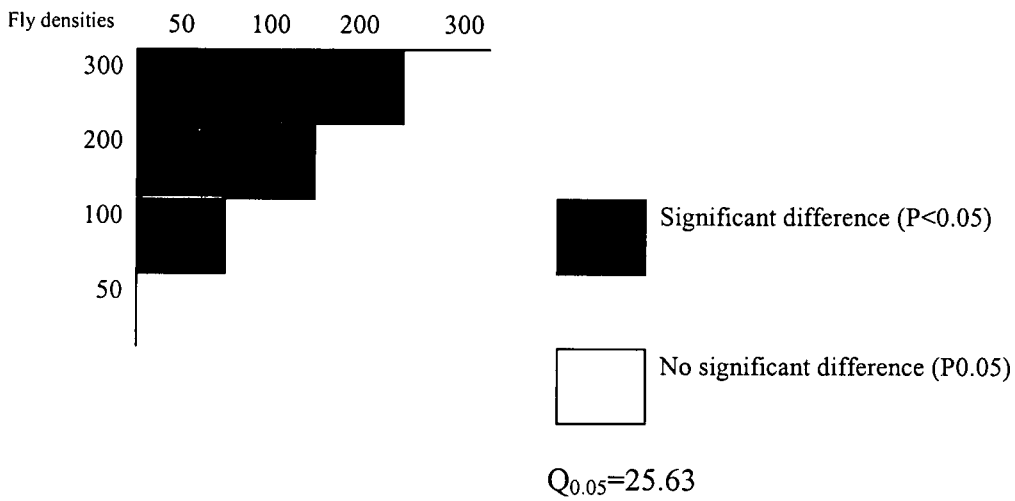


Figure A7.8: A schematic presentation of the significant differences in the number of Scatopsidae emerging from dung pats which contained different densities of these flies.

Table A7.9: Analysis of variance of the number of Sphaeroceridae flies that emerged from dung pats containing different densities of *Musca xanthomelas* flies.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	1121533.54	4	280383.386	6.59222315	0.00062407	2.68963163
Error	1275973.43	55	42532.4476			
Total	2397506.97	59				

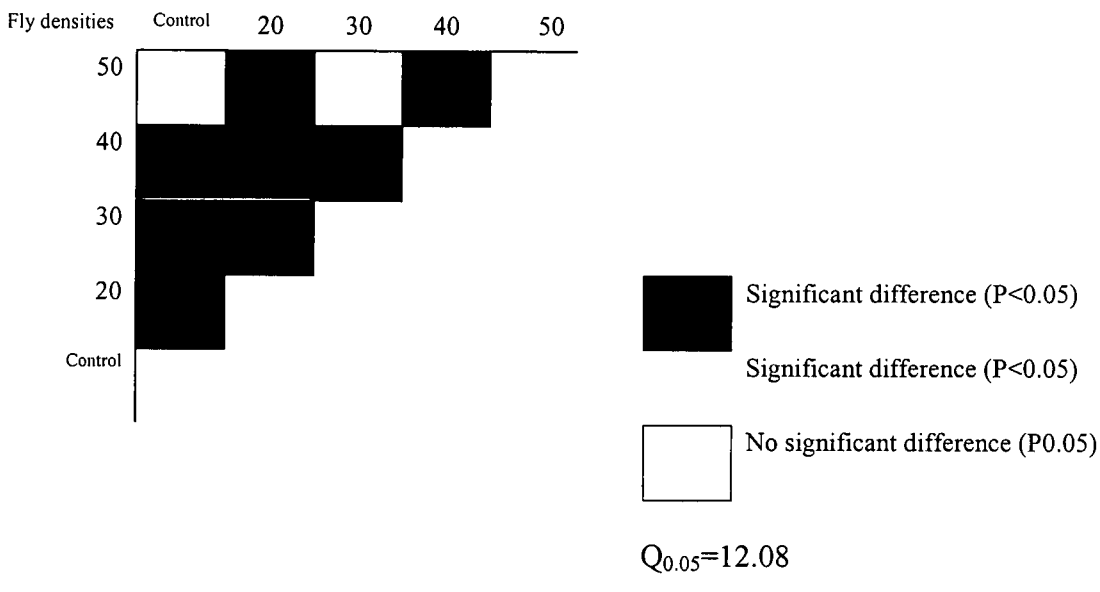


Figure A7.9: A schematic presentation of the significant differences in the number of Sphaeroceridae emerging from dung pats which contained different densities of *Musca xanthomelas* flies

Table A7.10: Analysis of variance of the number of Muscidae flies that emerged from dung pats containing different densities of *Musca xanthomelas* flies.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	710.392857	4	236.797619	5.7538328	0.00410836	3.00878611
Error	987.714286	35	41.1547619			
Total	1698.10714	39				

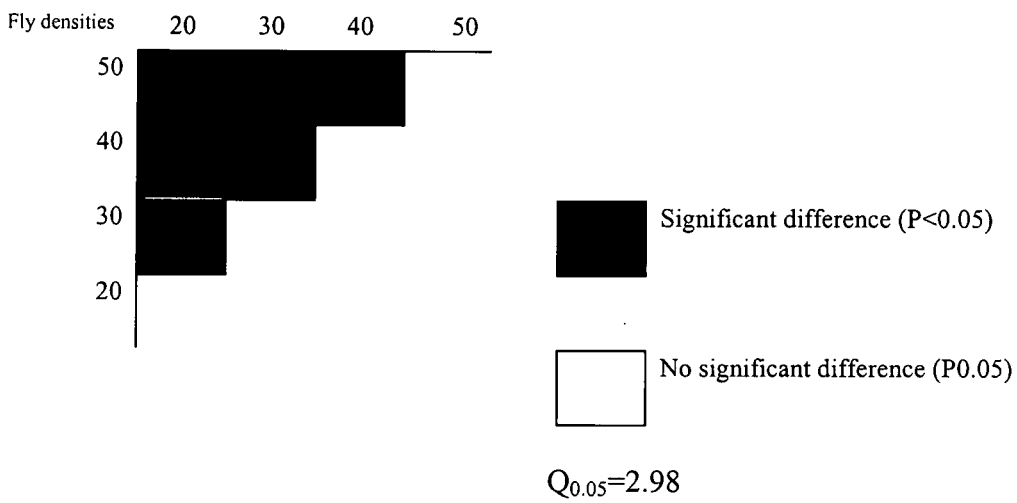


Figure A7.10: A schematic presentation of the significant differences in the number of Muscidae emerging from dung pats which contained different densities of these flies.

Table A7.11: Analysis of variance of the number of Sphaeroceridae flies that emerged from dung pats containing different densities of mites.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	1758957.54	3	586319.179	37.2336503	3.452E-09	3.00878611
Error	377928.571	56	15747.0238			
Total	2136886.11	59				

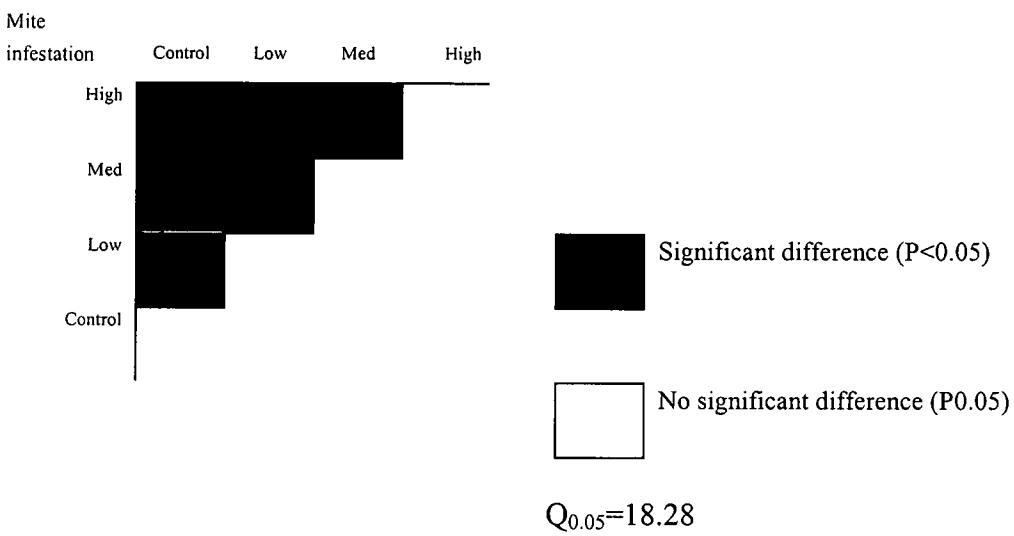


Figure A7.11: A schematic presentation of the significant differences in the number of Sphaeroceridae emerging from dung pats which contained different densities of mites.

CHAPTER 8

THE IMPACT OF POSSIBLE CONTROL AGENTS ON SPHAEROCERIDAE AT FEEDLOTS.

8.1 INTRODUCTION

The complex of fauna that uses animal excreta, particularly that of cattle, has attracted the attention of biologists worldwide (Hammer, 1941; Mohr, 1943; Poorbaugh, 1966; Blume, 1972; Rohacèk, 1983). In many parts of the world dung fauna includes the larvae of Diptera that are pests of cattle or domestic stock, either as blood-sucking insects or as nuisance flies swarming around the eyes or feeding on the exudates of sores (Schmidt & Kunz, 1980). Sphaeroceridae, in particular, constitute a serious problem at feedlots throughout South Africa and therefore it became important to find a suitable chemical means to control these flies at feedlots more effectively.

Prior to the discovery of the insecticidal value of DDT, sanitation had long been recognized as one of the principal basic fly control measures (Quarterman *et al.*, 1949). Municipal laws and regulations governing the maintenance of horses, cattle and other domestic livestock within city limits had long since removed the most prolific sources of fly breeding in most cities (Quarterman *et al.*, 1949). Unfortunately the size of feedlots in South Africa and the amount of dung produced by the cattle every day make it impossible to control Sphaeroceridae by means of sanitation principals only. The reason for this is mainly because the removal of dung from the camps is labour-intensive, expensive and difficult to maintain, although it is done once a year at most of the feedlots. Other Sphaeroceridae control measures that have been used in the past include the application of large volumes of sea water to the breeding sites to control the flies before their mass breeding season (Mihara *et al.*, 1989).

Strong (1992) maintained that since chlorinated hydrocarbon insecticides were marketed for commercial use against pests of medical, veterinary and horticultural importance, research and development have produced successive generations of insecticides of increasing power. This was done in order to meet new demands and overcome problems arising from insect resistance (Strong, 1992). Insecticides are of considerable value in agriculture, but unfortunately it is detrimental to the environment (Strong, 1992).

Since the major insect orders inhabiting cattle dung are Diptera and Coleoptera, it is not surprising that most observations on the impact of insecticides relate to these orders. According to Miller (1974), some of the pest Diptera species that were studied extensively includes the house fly *M. domestica* and the face fly *M. autumnalis*. Kunz *et al.*, (1977) investigated ways to control the horn fly *H. irritans,* while (Schmidt & Kunz, 1980) studied the stable fly *S. calcitrans.* Recently the Australian bush fly *M. vetustissima* received some attention by Ridsdill-Smith (1988).

The success of biological control agents was discussed in a previous chapter (see chapter 7). Due to the weak performance of the organisms as biological control agents against Sphaeroceridae and the poor results that were obtained, the only other alternative that remained was chemical control of Sphaeroceridae at the feedlot. This chapter deals with the effect of seven different insecticides and chemicals as well as a bacterium on the development of the immature stages and survival of adult Sphaeroceridae on feedlot dung in tests that were conducted in the laboratory and at Blokhuis feedlot outside Harrismith (see Figs. 3.1 & 3.2).

8.2 MATERIAL AND METHODS

The evaluation of different insecticides was conducted in the laboratory before any field trials. Only those that proved to be successful in the laboratory were reported in the results and underwent further tests under natural field conditions at the feedlot. A

bacterial medium *Bacillus thuringiensis* var. *israelensis* known as Vectobac 12AS was also tested as a control agent against Sphaeroceridae flies. Although VectoBac 12AS is a biological control agent and not a chemical product like the others used in this study, it was included in this section only because the experimental procedure, data processing and evaluation were done in the same manner. Seven other chemicals in either liquid or granular from, including two plant fertilizers, were tested in this study. A summary of the dosages that were used is given in Table 8.1.

The experimental procedures for all eight laboratory experiments were the same. Dung was collected at Blokhuis feedlot and placed in large plastic containers (18 cm x 11 cm x 9 cm). Each of the dilutions of the different chemicals that were prepared was sprayed evenly onto the dung in the plastic containers with a spraying-device in three different volumes. These volumes included a low volume (1 litre/m^2), a medium volume (3 litre/m^2) and a high volume (5 litre/m^2). A control, where only distilled water was added to the dung, was also included for each of the experiments. The dung on which the chemicals was sprayed, was then carefully transferred to small plastic containers (Apex vials No. 8 with a surface area of 20 mm^2) which were then covered with perforated stoppers to allow air ventilation.

Since the two Sphaeroceridae species, *C. vagans* and *C. hirtula* co-existed at the feedlot, no attempt was made to separate any of the stages in the life-cycle of the flies. The main aim of these studies was to evaluate the efficiency of the different control products on the sphaerocerid flies. Therefore it was not be necessary to separate the two species.

Fifty eggs were collected from laboratory-reared sphaerocerid colonies. These eggs were transferred to the small plastic containers containing the treated dung. The number of eggs that hatched was monitored after two days.

Table 8.1. The chemicals and dosages used during tests to evaluate the efficiency of different chemicals on Sphaeroceridae mortality.

Commercial name	Chemical compound	Recommended dosage	Dosage range tested	Manufacterer
Scatterkill	Piperonyl butoxide / Cypermethrin	10 g/m^2	2.5-100 g/m^2	Effekticide
Neporex	Cyromazine	25g/l	6.3-100 g/l	Ciba-Geigy
Vectobac 12AS	*Bacillus thuringiensis* var. *israelensis*	0.05-0.25 ml/m^2	0.05-2.5 ml/m^2 in 1 liter distilled water	Abbott laboratories
Nomolt	Teflubenzuron	0.02 µl/l	$2x10^{-6}$-200 $µl/l^1$	CelaMerck
Jeyes fluid	Carbolic acid	N/A	30-480 ml/l^1	Adcock-Ingram Pharmaceuticals
Ammonium	Ammonium	N/A	20-100% solutions of concentrated liquid NH_3	Merck
Ammonium sulphate	Ammonium sulphate	50 g/m^2	12.5-500 g/m^2	Kynoch
Ureum	Ureum	35 g/m^2	8.8-350 g/m^2	Kynoch

Similarly 50 first instar larvae and 50 pupae, both approximately 12 hours old, were respectively collected from the laboratory colonies and transferred to the prepared small containers with treated dung. Development and survival of larvae and pupae in the treated dung were monitored until both completed their development.

The life expectancy of adult flies on dung treated with the different chemicals was also tested by individually placing one-day-old adult flies of both species into Apex vials (No. 8) which were filled with the treated dung to a depth of 1 cm.

There were 10 replicates in each treatment and all the experiments with eggs, larvae, pupae and adults were repeated three times. These experiments were all conducted in a temperature-controlled incubator set at 24 ± 1°C with a day-night cycle of 12 hours light and 12 hours darkness.

The residual effect of Scatterkill after application to the dung was also determined. The reason for this was to determine the intervals between Scatterkill applications to dung at the feedlot. This was done in the laboratory by applying the standard application of Scatterkill granules (10 g/m^2) to feedlot dung. This dung was then carefully transferred to the small plastic containers and to Apex vials. These containers and vials were stored in the same temperature controlled incubators used for the other Scatterkill experiments for up to 16 weeks. Additional distilled water was added every third day to prevent the dung from drying out. Only the larvae and adults were tested. Fifty laboratory reared first instar larvae from both species were put into each of the plastic containers. Individual adult flies of both species were put into the Apex vials containing the Scatterkill treated dung of different ages. The intervals of larval or adult fly introduction after Scatterkill treatment were as follows: 1 week, 2 weeks, 3 weeks, 4 weeks, 6 weeks, 8 weeks, 12 weeks and 16 weeks. The development and survival of the larvae were monitored for the duration of the larval stage or until all the larvae had died. Adult survival was determined until all the flies were dead.

Scatterkill and Neporex were subsequently tested at the feedlot under natural summer field conditions in the sun. This was done at a site just outside a camp where sphaerocerid fly activity was high. Sphaeroceridae flies were collected with an insect sweeping net and approximately 1000 flies were transferred to each of the insect rearing cages (40 x 40 x 40 cm). Feedlot dung was placed into large metal pans (30 x 40 cm) to a depth of ± 2 cm and the dung was treated with the recommended dosages of Scatterkill and Neporex, which were 10 g/m^2 Scatterkill and 25 g/l Neporex. The pans containing the treated dung were put into separate rearing cages containing the flies. Observations were made daily and the percentage of flies that were still alive was determined. A control cage was also included in which the dung in the metal pans was untreated. The experiment was repeated three times.

A survey was also conducted at the feedlot to determine the effect of Scatterkill and Neporex on non-target organisms present in the feedlot dung. The recommended dosages of Scatterkill and Neporex were then applied separately - each to a 10 m^2 area of dung. One square meter of treated dung was then collected to a depth of 5 cm at four separate intervals *viz.* one day, two days, three days and one month after treatment. These dung samples were taken back to the laboratory at each interval, where the organisms present in the dung were identified and counted. Dung was also collected from an untreated area adjacent to the treated areas that served as a control. This experiment was repeated three times.

All data were subjected to probit analysis (SAS Institute 1985) where overlapping 95% confidence intervals were considered not significantly different.

8.3 RESULTS AND DISCUSSION

The results that were obtained for most of the substances that were tested (see Table 8.1) showed that it had no effect on any of the stages in the life cycle of Sphaeroceridae, and

it would therefore serve no purpose to present any of these results at this stage. However, two of these insecticides, namely Scatterkill (piperonyl butoxide/ cypermethrin) and Neporex (an insect growth regulator), showed positive results as far as the control of Sphaeroceridae flies are concerned.

8.3.1 Scatterkill

The percentage survival of eggs on dung treated with different concentrations of Scatterkill varied between 62% to 78% (Fig. 8.1). The lowest hatching percentage of 62 ± 5.7% was found at a Scatterkill concentration of 10 g/m^2 while the highest percentage of 78 ± 7.2% occurred at both 2 g/m^2 and 3 g/m^2 concentrations. All other hatching percentages were between 65% and 70%, whilst the control group showed a hatching percentage of 75 ± 6.4%. This was only slightly lower than the highest hatching percentages that were recorded (Fig. 8.1).

Analysis of variance ($F_{72;7}$=7.64) showed significant differences ($P<0.05$) in the hatching percentage of the eggs (Table A8.1). Tukey's test ($Q_{0.05}$=22.23) indicated that significantly higher hatching percentages occurred at Scatterkill concentrations of 2 g/m^2 and 3 g/m^2 than at all the other treatments, although these two concentrations did not differ significantly from each other (Fig. A8.1). The hatching percentage at the control treatment was also significantly higher than the other treatments, but significantly lower than both 2 g/m^2 and 3 g/m^2 Scatterkill treatments. No significant differences in egg survival were found between 0.25 g/m^2 and 1 g/m^2 Scatterkill concentrations (Fig A8.1).

The survival and development of larvae showed a different tendency. At the control group 68 ± 5.6% of the larvae survived, but at the other treatments it decreased to 23% and below. At Scatterkill concentrations between 0.25 g/m^2 and 2 g/m^2, larval survival varied from 13% to 23%, while at the other concentrations (3 g/m^2, 5g/m^2 and 10 g/m^2),

the percentage larval survival was only 9.0 ± 0.6%, 5.5 ± 0.2% and 1.5 ± 0.05% respectively (Fig. 8.1).

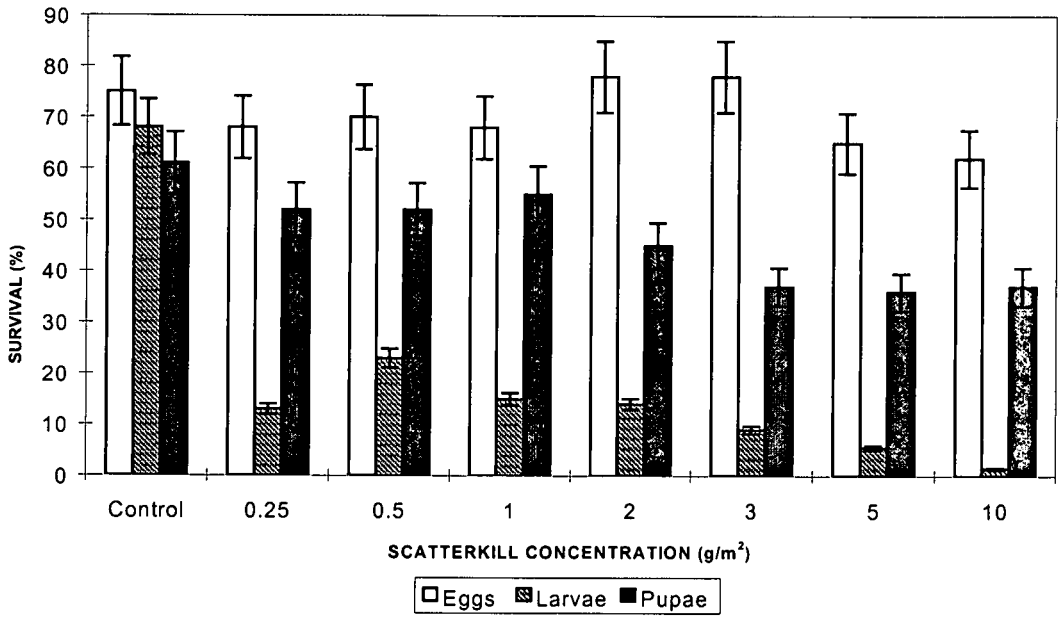


Figure 8.1: The survival of immature stages of Sphaeroceridae on dung treated with different concentrations of Scatterkill.

Analysis of variance ($F_{112;7}$=21.36) showed significant differences ($P<0.05$) in the survival of the larvae (Table A8.2). With Tukey's test ($Q_{0.05}$=20.04) it was shown that the larvae in the control treatment survived significantly better than all the other Scatterkill treatments (Fig. A8.2). The larval survival at 0.5 g/m^2 Scatterkill was also significantly better than all other Scatterkill treatments, but no significant differences were found between 0.25 g/m^2, 1 g/m^2 and 2 g/m^2 Scatterkill concentrations (Fig. A8.2).

The percentage pupal survival varied between 36% and 61% (Fig. 8.1). The lowest survival of 36 ± 2.8% occurred at a Scatterkill concentration of 5 g/m^2 while the highest survival of 58 ± 5.8% occurred at the control group. Pupal survival at a Scatterkill concentration of 1g/m^2 was also relatively high, in this case 55 ± 5.1%. At both 0.25

g/m^2 and 0.5 g/m^2 the percentage survival was 52%. All other concentrations resulted in survival rates of between 37% and 45%.

Analysis of variance ($F_{88;7}$=37.00) showed significant differences ($P<0.05$) in the survival of the pupae in Scatterkill treated dung (Table A8.3). Tukey's test ($Q_{0.05}$=10.79) indicated that pupal survival of the control group were significantly higher compare to all the other Scatterkill treatments (Fig. A8.3). Pupal survival at higher Scatterkill concentrations (3-10 g/m^2) were also significantly lower than at the lower Scatterkill concentrations, although the survival at these higher concentrations did not differ significantly from one another. No significant differences could also be found between 0.25 g/m^2 and 0.5 g/m^2 (Fig. A8.3).

The life expectancy of adult flies on dung treated with Scatterkill was very short (Fig. 8.2). Most of the flies only lived for one day, except between the 0.5 g/m^2 to 3 g/m^2 Scatterkill concentrations where some of the flies lived for two days. The control group survived for 16 ± 1.2 days. With analysis of variance ($F_{120;7}$=32.17), significant differences ($P<0.05$) in the life expectancy of the adult flies were shown (Table A8.4). Tukey's test ($Q_{0.05}$=2.01) showed that the life expectancy of adult flies of the control group was significantly higher compared to all the other Scatterkill treatments (Fig. A8.4). No significant differences in adult longevity were found between 0.25 g/m^2, 5 g/m^2 and 10 g/m^2 or between 0.5 g/m^2, 1 g/m^2, 2 g/m^2 and 3 g/m^2 Scatterkill concentrations.

Scatterkill proved to be effective against larvae over a period of 16 weeks after its initial application to the dung (Fig. 8.3). Larval survival was always below 4%, even after 16 weeks, when only 3.0 ± 0.2% of the larvae survived. At 4 and 6 weeks, larval survival was only 2%, while at the one-week interval, only 4.0 ± 0.25 % of the larvae survived.

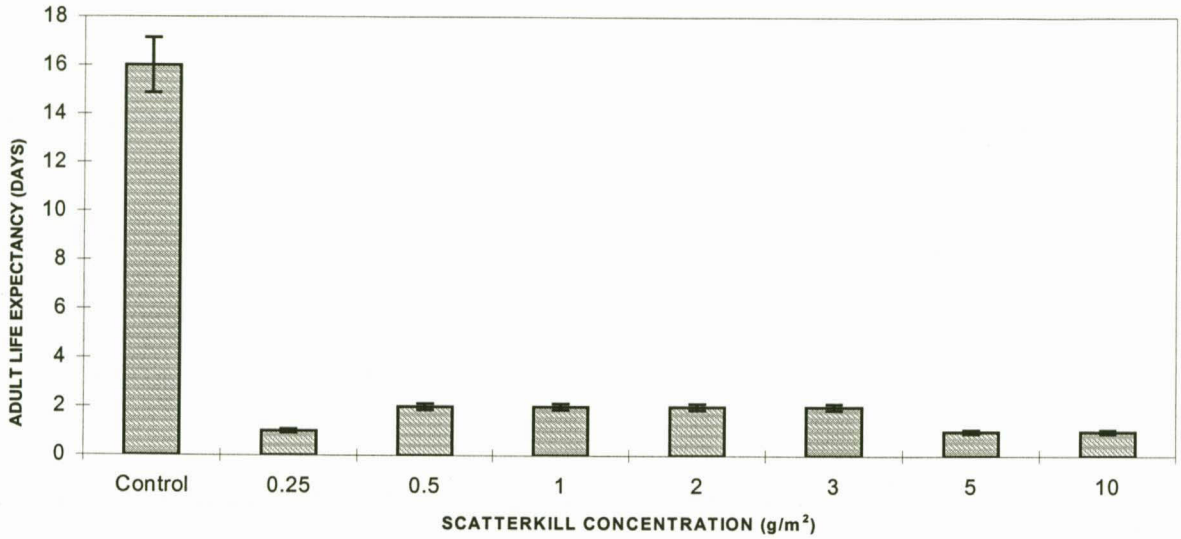


Figure 8.2: The life expectancy of adult Sphaeroceridae on dung treated with different concentrations of Scatterkill.

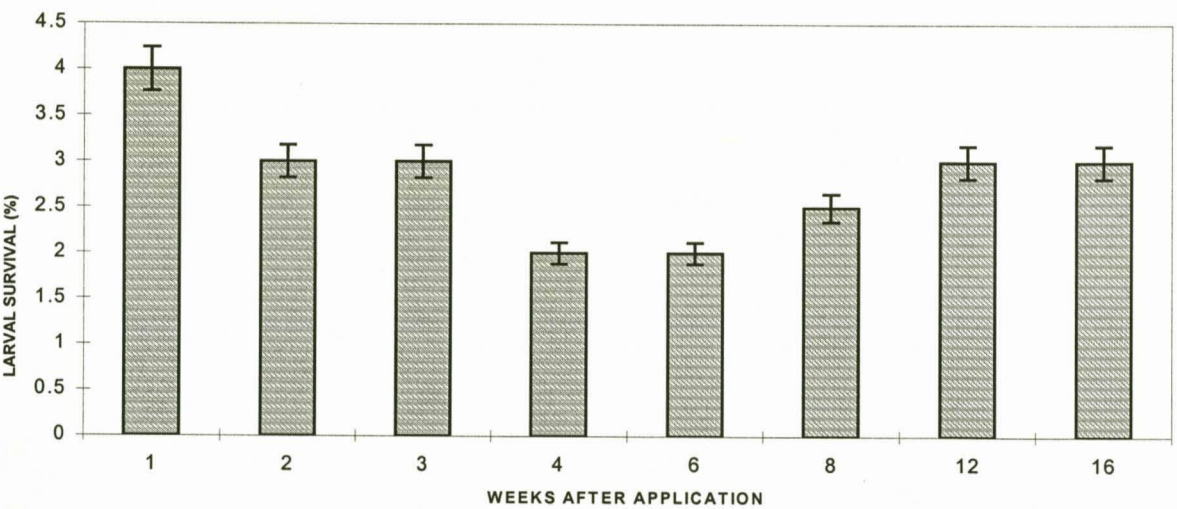


Figure 8.3: The efficacy of Scatterkill in controlling Sphaeroceridae larvae over an extended period.

Scatterkill is an insecticide formulation of small white granules registered for use against fly eggs, maggots and adults, as well as other insects such as crickets, ants and termites on lawns. Scatterkill consists of piperonyl butoxide (15 g/kg) and cypermethrin (3g/kg). The cypermethrin is a synthetic pyrethrin. It has to be applied evenly to substrates such as manure or compost heaps at a recommended dosage of 10 g/m^2. However, whether intimate mixing of this insecticide into the dung medium would have had any additional effect on the larvae and adult flies was not determined.

Pyrethrin sprays are ideal home insecticides because of their extremely rapid knockdown and are probably the safest insecticides known to man and his domestic animals (Lehman, 1949). When pyrethrins are used on their own, downed insects may recover and return to strike again, and consequently the synergists were included for the sole purpose of preventing the survival of insects (Lehman, 1949). The synergist thus prevents the insect from degrading pyrethrins and also from recovering after injury (Lehman, 1949).

Bruce & Decker (1950) found that by repeated treatment of the insect larvae and adults with insecticides containing dieldrin, para-oxon and pyrethrins, strains showing tolerance to these chemicals were developed. Furthermore, strains that were resistant to pyrethrins (and also to piperonyl butoxide) proved to be generally tolerant to all insecticides (Bruce & Decker, 1950).

Results showed that Scatterkill had very little effect on the development and hatching of eggs and that even at very high Scatterkill dosages, more than 60% of the eggs still hatched. No experimental work was done to test the permeability of the Sphaeroceridae egg chorion for Scatterkill or any other substances. However, it was assumed Scatterkill could not penetrate the chorion of the eggs and therefore did not affect the developing embryos inside the eggs.

However, as far as the larvae are concerned, study results have clearly indicated that Scatterkill could provide a solution to the Sphaeroceridae problem at the feedlot because of its effectiveness as a larval control agent. Indications are that the lethal effects of Scatterkill were exerted mainly on the larval stages of Sphaeroceridae. Observations that were made during laboratory experiments showed that the few larvae that reached the pupal stage, were severely deformed. The pupae were also visibly smaller in comparison to the untreated control pupae and would probably not have developed to adulthood. These findings are in agreement with those of Scott *et al.* (1991) who indicated that a combination of pyrethrins and piperonyl butoxide was extremely toxic to both *M. domestica* and its parasitoid *Muscidifurax raptor* Girault & Sanders (Hymenoptera: Pteromalidae) in New York, USA.

Results from experiments where pupae were exposed to Scatterkill treated dung showed that pupae were only slightly influenced by this insecticide. The fact that the pupae were protected from Scatterkill by a puparium and also because they did not consume any of the treated dung, might both have contributed to their survival.

Adult fly eradication by using Scatterkill also proved to be very quick and successful. Most of the flies died within the first 24 hours, and the few individuals that survived beyond this period, died within 36 hours. The chances that adult flies that were exposed to Scatterkill would be able to mate and oviposit are also extremely remote because of the very short survival period. These results are in line with those of Scott *et al.* (1991) who were able to demonstrate the highly toxic effect of pyrethrin and piperonyl butoxide on adult *M. domestica* at Ithaca, New York.

Scatterkill seemed to remain active in dung for a period of up to four months. Scatterkill would undoubtedly be effective beyond this four-month period, but for the purposes of this experiment it was unnecessary to test its effectiveness for a longer period. Repopulation of dung containing insecticides such as Ivermectin and Scatterkill by

coprophagous fly larvae as assumed by McKeand *et al.* (1988) is unlikely because of the persistence of this insecticides in the dung. However, the intervals of Scatterkill applications at feedlots would definitely have to be shorter than this because of the large amount of fresh dung produced by cattle each day. The results of this study indicated that at feedlots, or any other similar situations where animal waste accumulates, treatment on a weekly basis, only during times of heavy fly infestations, should provide adequate control of Sphaeroceridae during these periods. Another reason why Scatterkill treatment should continue on a weekly basis is because during times of heavy fly infestations, immigration of newly emerged flies from nearby sources cannot be ruled out. These flies could then possibly utilize the fresh untreated dung.

A delay in the decomposition of Scatterkill treated dung could further complicate control measures, as Madsen *et al.* (1990) have reported to be the case when dung pats were treated with ivermectin. They found that decomposition of dung with ivermectin had taken up to 20 days after treatment, and this phenomenon was mediated indirectly by reduced insect activity (Madsen *et al.*, 1990). However, fly larvae contribute only little to dung decomposition by direct intake of organic matter (Holter, 1979). Ivermectin-induced suppression of dung beetles was mainly responsible for a decrease in dung decomposition (Madsen *et al.*, 1990). This phenomenon would have no impact on dung decomposition at feedlots though, simply because no dung beetles are present in feedlot dung. This could imply that the decomposition rate of feedlot dung would be the same, regardless of whether Scatterkill gets applied to the dung or not.

8.3.2 Neporex

The hatching percentages of eggs on dung treated with Neporex were between 68% and 90% (Fig. 8.4). The lowest hatching percentage of 68 ± 4.9% occurred at a concentration of 6.3 g/l at high application, while the highest hatching percentage occurred at 12.5 g/l at low application and at 25 g/l, at both low and medium applications, where the average

hatching percentages recorded were 87 ± 7.1%, 87 ± 6.9% and 90 ± 7.4% respectively. All the other treatments and applications resulted in hatching percentages for the eggs varying between 70% and 85% (Fig. 8.4). The hatching percentage of the control group was 85 ± 6.2%.

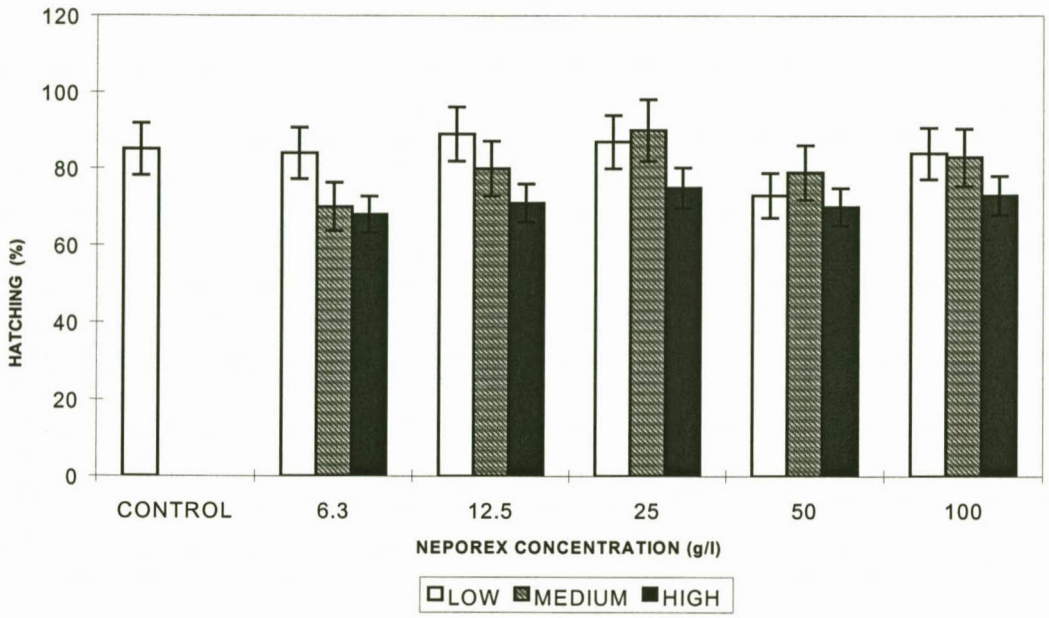


Figure 8.4: The percentage Sphaeroceridae eggs that hatched on dung treated with different concentrations of Neporex.

With analysis of variance significant differences ($P<0.05$) were shown in the hatching percentages of the eggs at low ($F_{36;5}=4.23$) (Table A8.5), medium ($F_{36;5}=3.18$) (Table A8.6) and high applications ($F_{36;5}=4.98$) (Table A8.7). Tukey's test ($Q_{0.05}=2.01$) showed that the percentage egg hatching at 50g/l low application was significantly lower compared to the rest of the applications. No significant differences in hatching were found between the control, 6.3 g/l, 25 g/l or 100 g/l or between 12.5 g/l and 25 g/l concentrations (Fig. A8.5). For the medium applications it was shown by a Tukey's test ($Q_{0.05}=13.44$) that hatching percentages at 25 g/l were significantly higher compared to the rest of the concentrations (except for the control), while egg hatching at 6.3 g/l

proved to be significantly lower than the rest. In this case no significant differences were found between 12.5 g/l and 50 g/l or between the control and 25 g/l (Fig. A8.6). As far as the high applications are concerned, Tukey's test ($Q_{0.05}$=8.87) indicated that hatching percentages at 25 g/l were significantly higher than the rest of the concentrations, except for the control repetition. No significant differences were shown in egg hatching between 6.3 g/l, 12.5 g/l, 50 g/l or 100 g/l Neporex concentrations (Fig. A8.7).

Survival and development of larvae in dung treated with Neporex ranged from 9% to 45%. In the control group, 71 ± 5.4% of the larvae survived (Fig. 8.5). The lowest percentage survival occurred at 50 g/l at the medium application where 9.0 ± 0.9% of the larvae reached the pupal stage while the highest percentage survival of 45 ± 2.6% occurred at a concentration of 6.3 g/l, also at medium application. The rest of the treatments and applications resulted in percentage survival that ranged from 11% to 34% (Fig. 8.5). At higher Neporex concentrations (50 g/l - 100 g/l), larval survival was never above 15% at any of the applications (Fig 8.5).

Analysis of variance showed significant differences ($P<0.05$) in larval survival at low ($F_{48;5}$=42.88) (Table A8.8), medium ($F_{48;5}$=35.10) (Table A8.9) and high applications ($F_{48;5}$=53.93) (Table A8.10). Tukey's test ($Q_{0.05}$=35.21) showed that the percentage larval survival at the control repetition was significantly higher compared to the rest of the applications. No significant differences in larval survival were recorded between 6.3 g/l and 12.5 g/l or between 50 g/l and 100 g/l Neporex concentrations at low applications (Fig. A8.8). As far as the medium applications are concerned, it was shown by means of a Tukey's test ($Q_{0.05}$=18.31) that larval survival percentages at the control were again significantly higher compared to the rest of the concentrations, while significant differences in larval survival occurred between all the different Neporex concentrations (Fig. A8.9). For the high applications, Tukey's test ($Q_{0.05}$=19.98) also showed that larval survival at the control differed significantly from the rest of the Neporex concentrations.

However, no significant difference in larval survival was shown between 25 g/l and 100 g/l concentrations (Table A8.10).

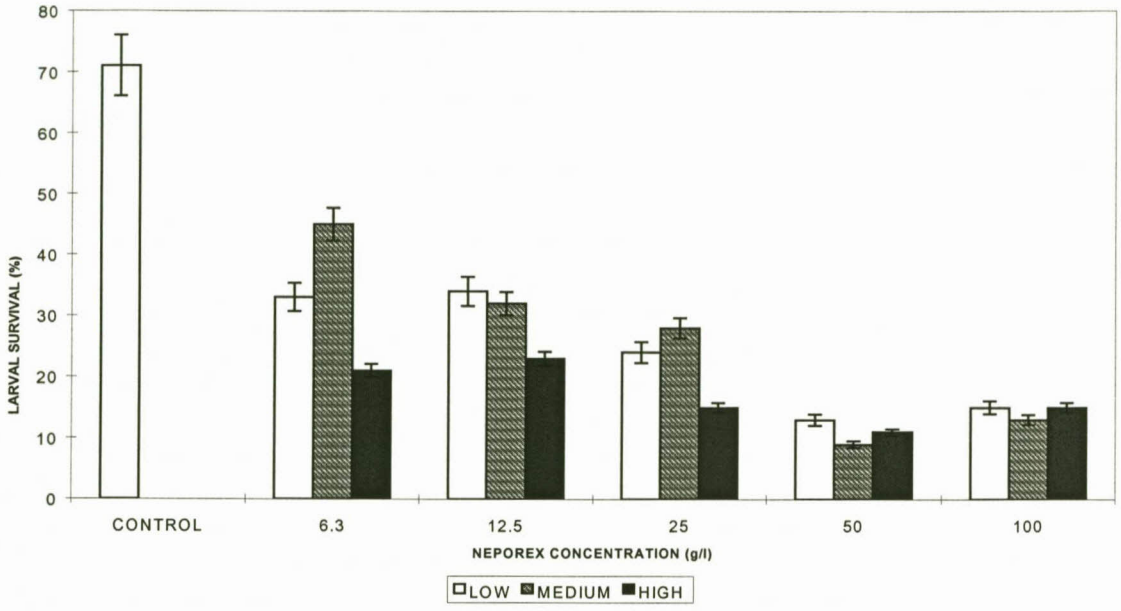


Figure 8.5: The percentage Sphaeroceridae larval survival on dung treated with different concentrations of Neporex.

Pupal survival ranged between 40% and 65%, with the control treatment showing a survival percentage of 66 ± 5.2% (Fig. 8.6). The lowest percentage survival for the pupae was 40 ± 2.4% at a concentration of 50 g/l at medium application, while the highest percentage survival of 65 ± 4.9% occurred at a concentration of 6.3 g/l at low application (Fig. 8.6).

With analysis of variance significant differences ($P<0.05$) in percentage pupal survival were shown in the at low ($F_{42;5}=23.62$) (Table A8.11), medium ($F_{42;5}=41.79$) (Table A8.12) and high applications ($F_{42;5}=7.32$) (Table A8.13). Tukey's test ($Q_{0.05}=22.67$) showed no significant differences in the percentage pupal survival between 12.5 g/l and 50 g/l Neporex concentrations at low application or between 6.3 g/l and the control

repetition (Fig. A8.11). For the medium Neporex applications, Tukey's test ($Q_{0.05}$=20.13) showed that significant differences in the percentage pupal survival existed between all concentrations except between 6.3 g/l and 100 g/l (Fig. A8.12). Tukey's test ($Q_{0.05}$=15.91) furthermore indicated that pupal survival at the control repetition was significantly higher than at any of the Neporex concentrations at high application. In this case no significant differences in pupal survival were recorded between 6.3 g/l, 12.5 g/l and 50 g/l (Fig. A8.13).

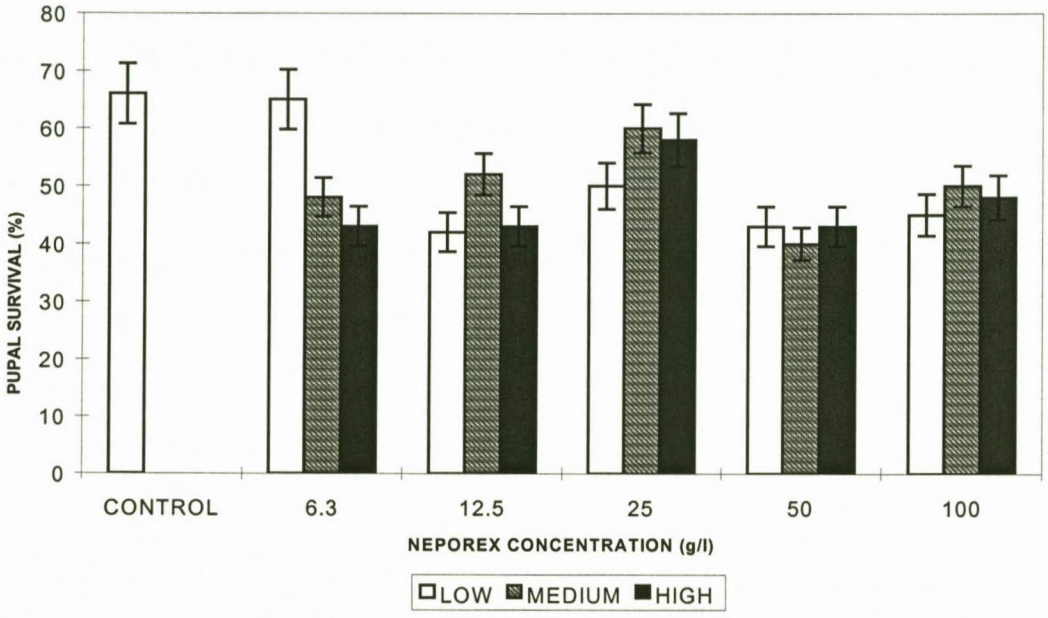


Figure 8.6: The percentage Sphaeroceridae pupae that survived on dung treated with different concentrations of Neporex.

The life expectancy of adult flies on dung treated with Neporex varied from 12 to 24 days (Fig. 8.7). The shortest survival of only 12 ± 1.3 days occurred at a concentration of 25 g/l at high application, while the longest survival was found at 6.3 g/l and 50 g/l, both at low applications, where the life expectancy of the adult flies were 24 ± 1.5 and 23 ± 1.6 days respectively (Fig. 8.7). The control treatment also showed a life expectancy of

24 ± 1.5 days, similar to the maximum longevity of adult sphaerocerids at 6.3 g/l and 50 g/l.

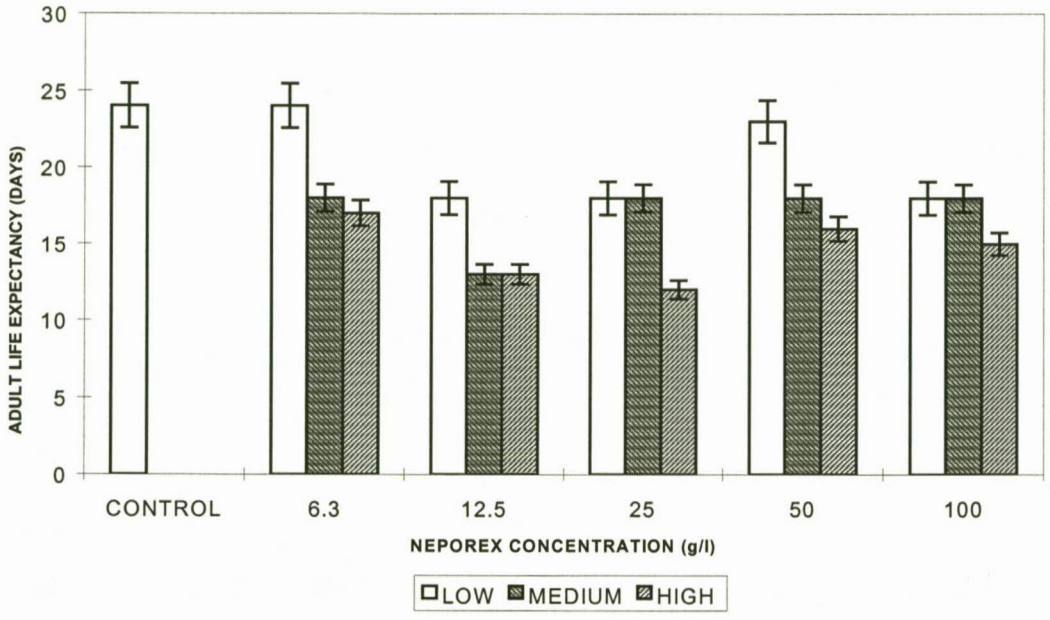


Figure 8.7: The life expectancy of adult Sphaeroceridae flies on dung treated with different concentrations of Neporex.

Analysis of variance showed that significant differences ($P<0.05$) in the life expectancy of adult Sphaeroceridae existed at low ($F_{48;5}=29.90$) (Table A8.14), medium ($F_{48;5}=80.20$) (Table A8.15) and high applications ($F_{48;5}=30.77$) (Table A8.16). Tukey's test ($Q_{0.05}=18.64$) showed that at low Neporex applications, the life expectancies of adult Sphaeroceridae differed significantly between the low and high concentrations. However, no significant differences were found between the control repetition and 6.3 g/l Neporex concentration or between life expectancies at 12.5 g/l, 25 g/l and 100 g/l (Fig. A8.14). For the medium applications, it was shown by a Tukey's test ($Q_{0.05}=21.22$) that adult life expectancies at the control were significantly higher compared to the rest of the concentrations while those at 12.5 g/l proved to be significantly lower than the rest. No significant differences were found between 6.3 g/l, 25 g/l, 50 g/l or 100 g/l (Fig.

A8.15). In the case of the high applications, Tukey's test ($Q_{0.05}$=28.53) again showed significant differences in adult life expectancies were shown between all the Neporex concentrations (Fig. A8.16).

Insect growth regulators have opened up new vistas in the control of arthropods of veterinary importance (Chamberlain, 1975). Neporex (Cyromazine) is one such insect growth regulator and their mechanism differs from that of conventional insecticides in that the compound destroys the developmental stages of numerous species of insects by preventing cuticle chitin formation during moultings during the larval stages (Farkas & Sounthone, 1985). Nelson *et al.* (1985) stated that the basic strategy in utilizing insect growth regulators is to interrupt the development and growth processes and thus inhibit the emergence of an adult population. The activity of one such insect growth regulator, diflubenzuron, was demonstrated by Elings & Dieperink (1974) in Lepidoptera and by Moore & Taft (1975) in the boll weevil, *Anthonomus grandis* Boheman. These insect growth regulators have a biological activity that mimics that of natural insect juvenile hormones (Schaefer & Wilder, 1972). Wright & Harris (1976) showed that the insect growth regulator diflubenzuron, [also known as Dimilin® WP-25 or Thompson-Hayward TH 6040 or N-(4-chlorophenyl)-N1-(2,6-difluorobenzoyl)urea] exerts its biological effect in the early stages of embryonic development and showed that the hatching of the first instar *H. irritans* larvae developing within the eggs were partially or completely inhibited. Several other insect growth regulators such as fenoxycarb, methoprene (Altosidâ), and Hoffman-La Roche Ro 20-3600 ((E)-[6,7-epoxy-3,7-dimethyl-2-nonenyl)oxy]1,2-(methyl-enedioxy) benzene) were reported to exhibit high levels of activity against mosquitoes and horn flies, while they also showed a good margin of safety to non-target biota including fish and birds (Mulla *et al.*, 1989).

Dissolved Neporex granules can be used on a variety of fly breeding sites. Manufacturers state that this insecticide prevents the development of fly larvae in breeding sites such as manure, refuse and compost heaps, dung pits, slurry and dung

channels, or soiled litter. It can also be used at poultries, pig stays, calf fattenings, dairies, feedlots and horse stables.

Results indicated that Neporex did not affect Sphaeroceridae eggs significantly, not even very high concentrations that were applied in large volumes. Although the manufacturers maintained that Neporex should be effective against flies breeding in dung, this was clearly not the case with Sphaeroceridae eggs. Neporex was probably unable to penetrate through the chorion of the eggs and therefore had no influence on the developing embryos. However, these results do not agree with the findings of Wright *et al.* (1978), who found that another insect growth regulator, diflubenzuron, reduced hatching of the stable fly, *S. calcitrans* and the house fly, *M. domestica* eggs in Texas, USA with as much as 97% when adult flies had been in contact with treated areas. They indicated with ^{14}C radiolable studies that diflubenzuron was present within the eggs of stable flies and house flies after topical treatment of females (Wright *et al.*, 1978). They furthermore stated that stable flies are highly sensitive to diflubenzuron during formation of first instar larvae inside the egg since diflubenzuron prevents chitin synthesis (Wright *et al.*, 1978). The reason for this discrepancy with the results of Wright *et al.* (1978) is unclear, but it could be that Neporex (cyromazine) does not have the same effect on Sphaeroceridae eggs as the diflubenzuron tested by Wright *et al.* (1978) had on stable fly and house fly eggs. On the other hand, Nelson *et al.* (1985) showed that the eggs and pupal stages were least sensitive to insect growth regulators because there was no penetration of any substance during these stages that could affect the developing embryo or pupae. Kunz *et al.* (1977) found that percentage horn fly eggs that hatch on dung treated with diflubenzuron was high in all tests that were conducted by them in Texas, USA.

As far as the efficacy of Neporex on larvae is concerned, the results showed that larval mortality in the laboratory studies was very good. In some instances fly larval development was reduced with up to 91%. The few larvae that survived had a short and

pinkish appearance. Some of the larvae also developed a bulge at the rear end of their bodies and they were all very weak, a clear indication that they were unhealthy. Very few of these larvae managed to reach the pupal stage. This is in accordance with findings of Budia & Vinuela (1996) who showed that the triazine compound cyromazine is an effective insect growth inhibitor that is toxic to *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae) larvae, mainly because it is orally administered to the larvae. They stated that when cyromazine was fed to *C. capitata* larvae, normal egg development occurred, although larval mortality reached 100% at the highest dosage applied (10 mg/ml) (Budia & Vinuela, 1996). In their studies Wright *et al.* (1978) also showed that larvae of the stable fly, *S. calcitrans*, were highly sensitive to diflubenzuron during the formation of the initial larval instar and at the time of the larval-pupal moult when the chitinous structure of the third instar larvae became the puparium. Kunz *et al.* (1977) also found that diflubenzuron treated dung often resulted in large numbers of dead first instar larvae in the dung, indicating that death occurred shortly after hatching. Demèny (1989) tested the larvicidal effectiveness of diflubenzuron on flies breeding in cattle houses in Hungary and found that, although the numbers of *M. domestica* and *C. hirtula* larvae present in dung samples taken were higher after treatment than before it, signs of damaged chitin synthesis were present in 80% of muscid pupae and in 9% of *C. hirtula* adults.

Results from the present study showed that Neporex did not affect pupae as much as it affected larvae. This could again be attributed to the protection that the puparium provided for the developing pupae, and as a result no penetration of Neporex occurred. These observations are in line with the view of Nelson *et al.* (1985) who stated that pupal stages were least sensitive to insect growth regulators. Demèny (1989) also maintained that *M. domestica* and *C. hirtula* pupae in calf houses in Hungary were less, if not at all, susceptible to insect growth regulators. Budia & Vinuela (1996) found that *C. capitata* pupal development was normal and numbers of emerged adults were not significantly different from those of the controls. On the other hand, Farkas & Sounthone

(1985) reported that Dimilin induced deformity of *Musca osiris* Wiedemann pupae in Hungary, but this could be due to the influence of this growth regulator on the larvae before pupation took place. Kunz *et al.* (1977) stated that diflubenzuron had no effect on horn fly adult emergence from pupae produced from manure that contained levels of the compound that were lethal to larvae.

The manufacturers of Neporex stated that it should not have an effect on adult insects. This was confirmed by the results obtained in the current study. Neporex had no serious lethal effect on Sphaeroceridae adults, even at very high doses. Although the actual amount of the growth inhibitor ingested by adult flies may vary from one individual to the next, it still had no effect on their survival. Therefore the reduction in adult numbers at the feedlot would be gradual. This is in general agreement with the findings of Wright & Harris (1976) who stated that diflubenzuron was non-toxic to adult horn flies in the USA since the treatments did not eliminate adult fly populations. However, Pochon & Casida (1983) suggested that effectiveness of cyromazine may be dependent on intrinsic species susceptibility, because they reported a 100% mortality in house fly, *M. domestica* adults at five days after the ingestion of cyromazine at a dose of 1 mg/ml. Likewise, Moreno *et al.* (1994) killed a large proportion of *Anastephra ludens* (Loew) (Diptera: Tephritidae) after two-day-old females fed on cyromazine laden food (0.125% - 8%), and stated that the effect was more conspicuous at higher dosages.

El-Oshard *et al.* (1985) were able to show that cyromazine excretion is rapid in flies, and that 95% of radiolabeled product could be recovered from treated *M. domestica* adults in less than 24 hours. Furthermore it is possible that adult flies could migrate from adjacent areas into the feedlot and therefore adult fly control should be practiced separately, over and above any Neporex treatments. Effects of Neporex fed to flies during their reproductive phase are not clear. Levot & Shipp (1984) found that when cyromazine was topically applied to the sheep blowfly *Lucilia cuprina* Wiedemann, fecundity of the

females remained normal. Similarly, no alteration of fertility has been observed in face fly *M. autumnalis* after the ingestion of low doses of cyromazine (Levot & Shipp, 1984).

The effect of Neporex on non-target organisms at the feedlot was a matter of concern, because Budia & Vinuela (1996) suggested that cyromazine could be a potential risk for some non-target Diptera. However, Jacas & Vinuela (1994) found in laboratory experiments in which cyromazine was tested on *Bactrocera oleae* (Gmelin) (Diptera; Tephritidae) that this growth inhibitor was selective in killing flies, although none of the braconid parasitoids were affected. This could suggest the potential compatibility with biological control of Sphaeroceridae at feedlots.

8.3.3 Field trials

Tests conducted with Scatterkill at the feedlot under natural field conditions proved as successful as in the laboratory trials. All adult flies were killed within two days after Scatterkill application to feedlot dung and after three days, all the flies in the rearing cages were killed (Table 8.2).

Table 8.2: The effect of Scatterkill and Neporex on adult Sphaeroceridae flies under natural conditions at the feedlot.

	Day 1	Day 2	Day 3
Scatterkill	± 2-5 % flies still alive	± 1-5 % flies still alive	All flies were dead
Neporex	± 95 - 99% flies still alive	± 95 - 99% flies still alive	± 80-90% flies still alive
Control	± 95 - 99% flies still alive	± 95 - 99% flies still alive	± 95 - 99% flies still alive

Field studies that were conducted at the feedlots to test the effect of Neporex under natural environmental conditions showed that the adult flies were not severely affected. The majority of the flies that were put into the insect rearing cages were still alive after three days (Table 8.2). This corresponded with the results from the laboratory experiments that showed that Neporex had very little influence on the adult Sphaeroceridae (Fig. 8.7).

Chamberlain (1988) suggested that concentrations of chemicals required for mortality of insects in the field should be greater than in laboratory tests because larval contact with Scatterkill in the laboratory was immediate, while in field tests, Scatterkill either had to penetrate the dung or larvae had to come to the top one or two centimeters of the dung before contact was made. This could explain why even the lowest dosage of 0.25 g/m^2 proved to be effective against both larvae and adult flies in the laboratory tests. The recommended dosage of 10 g/m^2 was therefore strictly adhered to when the Scatterkill was applied to the dung during the field tests at the feedlot. Most of the time Sphaeroceridae larvae were restricted to the surface of the medium and there was no need for Scatterkill to penetrate deep into the medium.

Many bird species were observed at the feedlot and the toxicity of Scatterkill to them was of some concern. According to Lehman (1948), the pyrethrin synergists in Scatterkill, *i.e.* cypermethrin, piperonyl butoxide and n-propyl isome, show a low level of acute toxicity, and oral LD50 ranges from 7500 to 11500 mg/kg in either compound. He furthermore stated that although they are not irritant to the skin, multiple consumption of 200 mg/kg doses may be fatal to laboratory animals (Lehman, 1948). Griffin (1973) stated that birds are resistant to the action of pyrethrins and pyrethroids, although fish are extremely sensitive. He also mentioned that the low toxicity in mammals is primarily due to too rapid metabolic breakdown, ester cleavage and then rapid oxidation (Griffin, 1973).

At South African feedlots, fly larvae are most numerous in habitats that were not routinely trod upon by cattle. Soil substrates are apparently compacted tightly enough under the weight of cattle to kill fly larvae developing within. Enabling feedlot cattle to walk on manure-laden soil containing fly larvae has been recommended as a fly control technique (Hogsette, 1996). However, Skoda *et al.* (1993) consistently found small numbers of house fly larvae in general lot areas used daily by cattle. Meyer & Schultz (1990) also reported large concentrations of fly larvae on California dairies in moist areas near water troughs and in stacked manure, but moderate numbers were recovered from lots occupied by animals. Chemical control therefore seems like the most appropriate control measure in this case. It is therefore essential to map the areas of larval fly development at these confinement cattle facilities and predict the contribution that these areas make to the total adult fly population, or else fly management will remain an elusive proposition. So far several areas at the feedlot were identified as major sources of Sphaeroceridae production. These include manure under fencelines, drainage ditches and spilled feed along the feeding troughs. These areas should therefore be targeted in particular when chemicals are applied for control purposes.

8.3.4 Non-target organisms

Species diversity inside the feedlot was extremely low. Results in Table 8.3 showed that apart from Sphaeroceridae, Muscidae and mites, there were not many other organisms present in the dung inside the feedlot camps. The only other organisms encountered were Syrphidae larvae and pupae and a spider species. The Staphylinidae and Scatopsidae present at the feedlot and which were used in biological control experiments (see 7.3.2 and 7.3.3), occurred only in the drier dung outside the camps. Treatment of dung inside the feedlot would therefore not present a serious ecological hazard, since only a few different organisms inside the feedlot camps would be affected. Besides, during the experiments with Scatterkill in the laboratory, it was noted that the mites and nematodes

in the dung were still alive long after the Sphaeroceridae larvae and adults were killed. It thus seems as if not all living organisms will in fact be affected by the Scatterkill.

Table 8.3: Diversity and number of organisms present in feedlot dung (1 m^2 to a depth of 5 cm) before and after treatment with Scatterkill and Neporex.

Scatterkill (10 g/m^2)	Control	Day 1	Day 2	Day 3	1 Month
Sphaeroceridae larvae	42	-	-	-	8
Sphaeroceridae pupae	47	13	6	5	2
Muscidae larvae	6	-	4	4	-
Muscidae pupae	7	1	6	1	-
Muscidae pupae	15	18	2	4	2
Syrphidae larvae	-	-	1	5	-
Syrphidae pupae	-	-	-	1	-
Neporex (25 g/l on 1m^2)	**Control**	**Day 1**	**Day 2**	**Day 3**	**1 Month**
Sphaeroceridae larvae	42	-	-	3	2
Sphaeroceridae pupae	60	48	47	21	7
Muscidae eggs	42	46	-	-	-
Muscidae larvae	6	-	-	-	1
Muscidae pupae	7	-	3	1	-
Mites	5	2	15	13	16
Linyphidae(spider)	-	-	2	-	-

The chemical control program succeeded in its main objectives. The primary aim was to find an effective way of controlling Sphaeroceridae flies at South African feedlots. Some of the chemicals that were tested, such as Nomolt and ureum plant fertilizer, had no effect on any of the immature stages in the life cycle of the Sphaeroceridae nor on the

adult flies, while ammonium influenced both the eggs and the pupae negatively. Larvae were the most vulnerable to any chemical application onto the dung. Scatterkill proved to be the most effective insecticide because of its effectiveness against larvae and adults alike, both in the laboratory and at the feedlot. Furthermore, the period of its effectiveness between applications was very extended. Tests showed that spraying of chemicals at the feedlot would also not cause any ecological damage, as dung fauna diversity inside the camps was extremely low. Neporex was also very effective against larvae, but had no serious effect on adults, which would implicate that eradication of flies at the feedlot would at most only be gradual.

8.4 APPENDIX

Table A8.1: Analysis of variance of the survival of Sphaeroceridae eggs on dung treated with different Scatterkill concentrations.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	9217.26786	7	1316.75255	7.64046657	3.5083E-06	2.20743601
Error	8272.28571	72	172.339286			
Total	17489.5536	79				

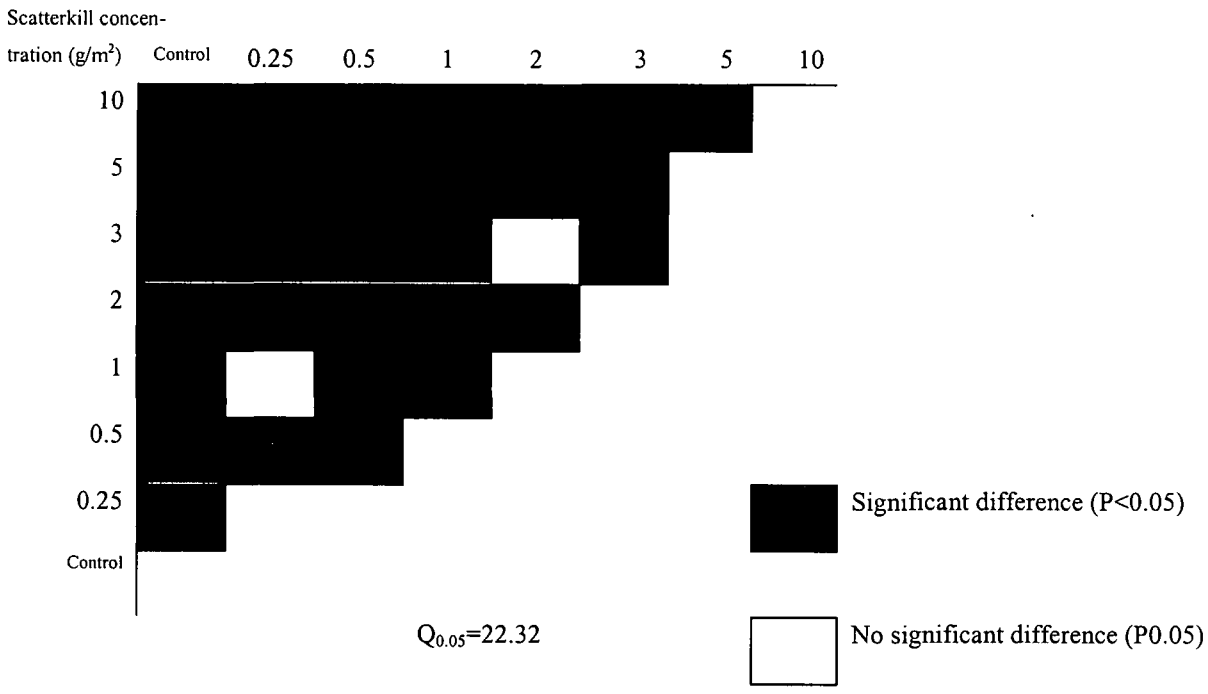


Figure A8.1: A schematic presentation of the significant differences in survival of Sphaeroceridae eggs on dung treated with different Scatterkill concentrations.

Table A8.2: Analysis of variance of the survival of Sphaeroceridae larvae on dung treated with different Scatterkill concentrations.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	30813.75	7	4401.96429	21.3644374	2.7222E-15	2.13965734
Error	14835	112	206.041667			
Total	45648.75	119				

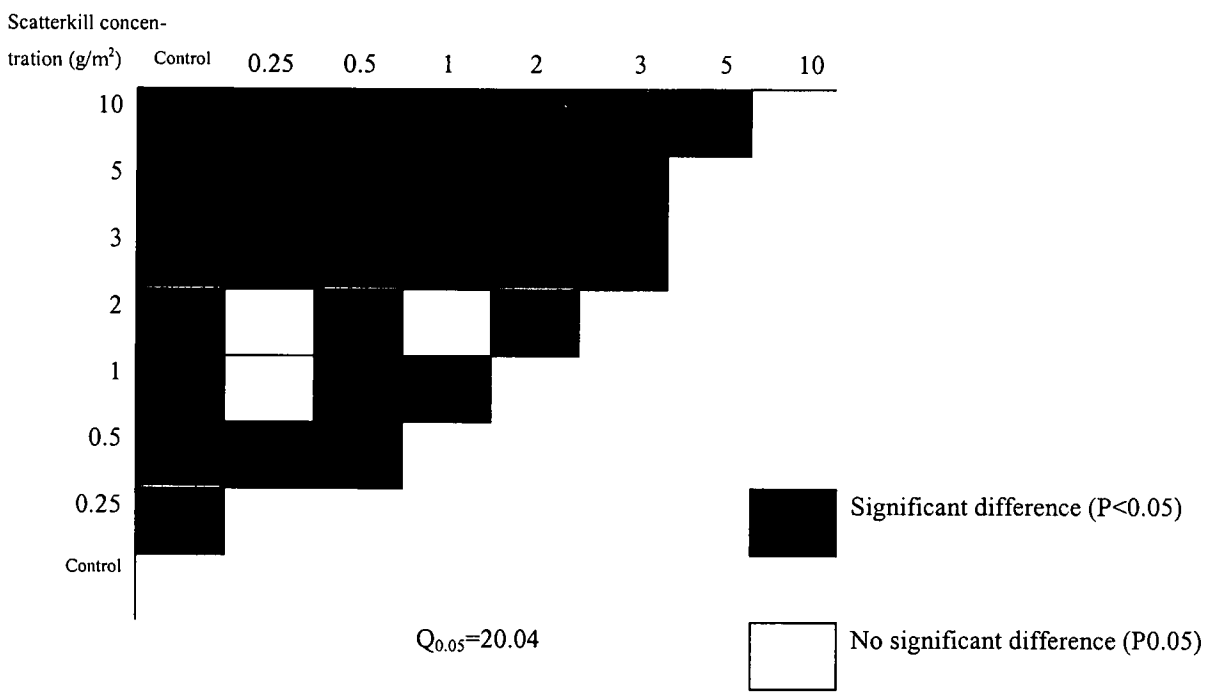


Figure A8.2: A schematic presentation of the significant differences in survival of Sphaeroceridae larvae on dung treated with different Scatterkill concentrations.

Table A8.3: Analysis of variance of the survival of Sphaeroceridae pupae on dung treated with different Scatterkill concentrations.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	10520.9821	7	1502.99745	36.9968603	3.0738E-17	2.20743601
Error	1950	88	40.625			
Total	12470.9821	95				

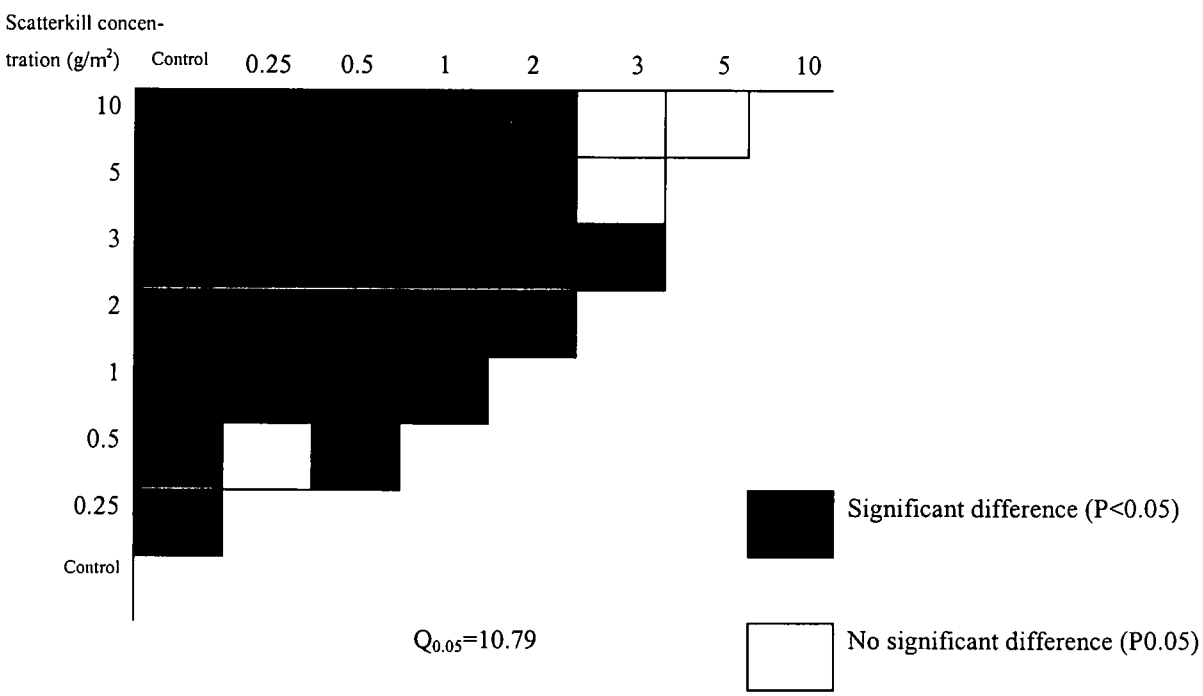


Figure A8.3: A schematic presentation of the significant differences in survival of Sphaeroceridae pupae on dung treated with different Scatterkill concentrations.

Table A8.4: Analysis of variance of the survival of Sphaeroceridae adults on dung treated with different Scatterkill concentrations.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	584.8	7	83.5428571	32.1662338	9.2221E-20	2.13965734
Error	187	120	2.59722222			
Total	771.8	127				

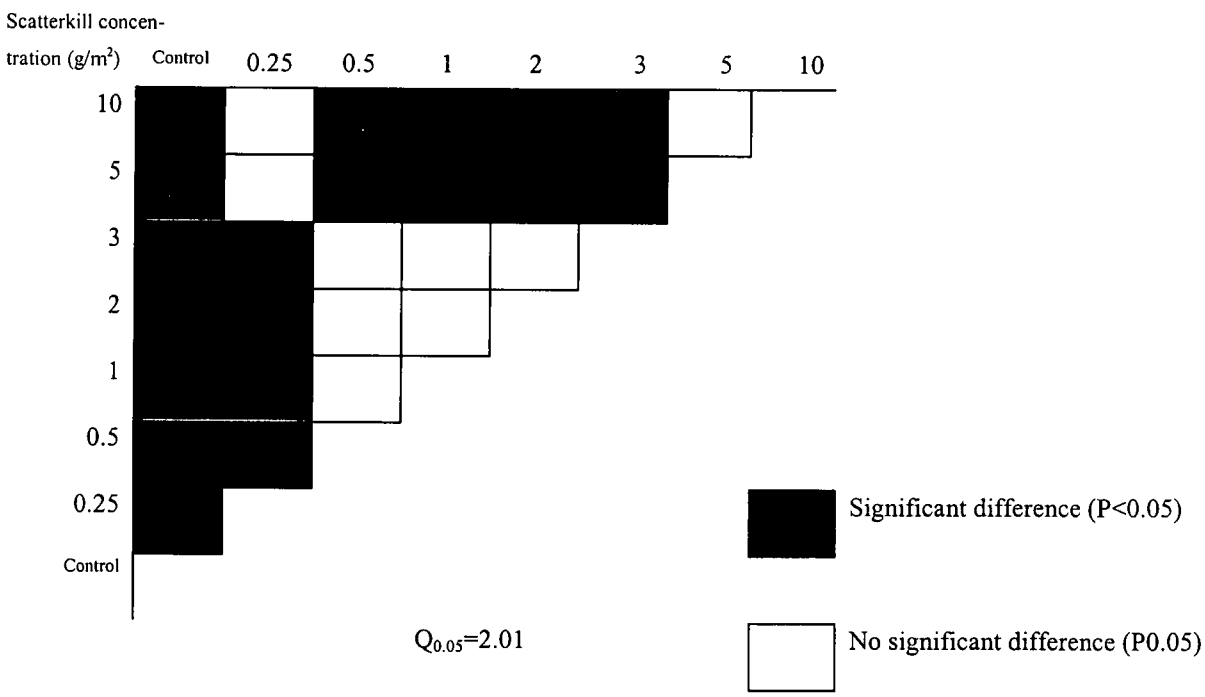


Figure A8.4: A schematic presentation of the significant differences in survival of Sphaeroceridae adult flies on dung treated with different Scatterkill concentrations.

Table A8.5: Analysis of variance of the survival of Sphaeroceridae eggs on dung treated with different concentrations of Neporex at low applications.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	1104.97619	5	220.995238	4.23182371	0.00396534	2.47716514
Error	1880	36	52.2222222			
Total	2984.97619	41				

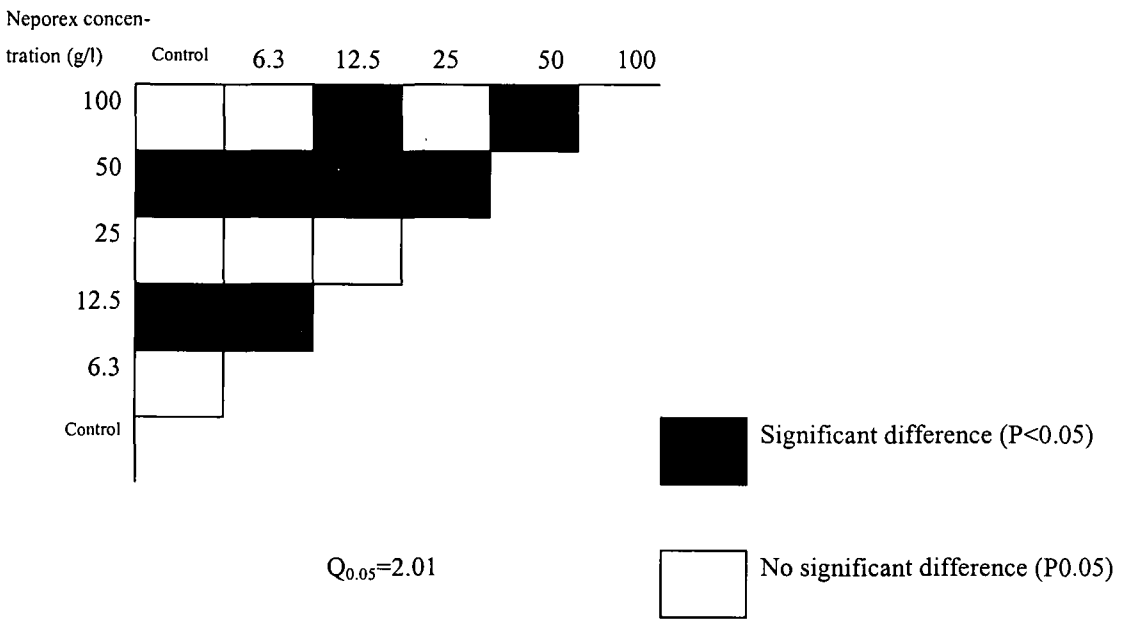


Figure A8.5: A schematic presentation of the significant differences in survival of Sphaeroceridae eggs on dung treated with different concentrations of Neporex at low applications.

Table A8.6: Analysis of variance of the survival of Sphaeroceridae eggs on dung treated with different concentrations of Neporex at medium applications.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	1446.40476	5	289.280952	3.18085348	0.017665	2.47716514
Error	3274	36	90.9444444			
Total	4720.40476	41				

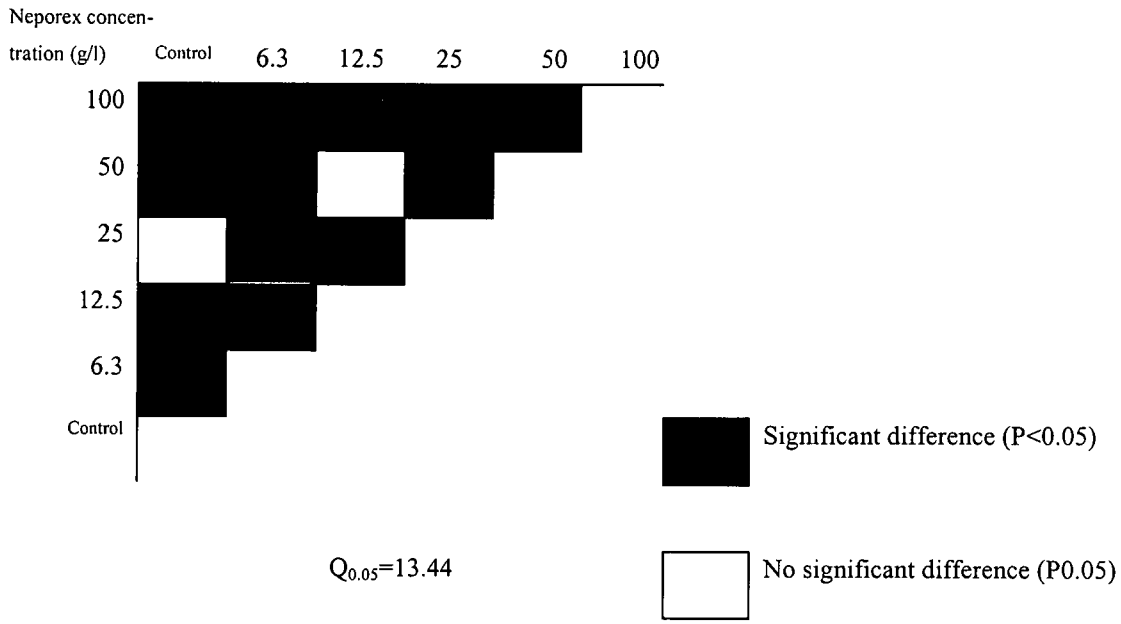


Figure A8.6: A schematic presentation of the significant differences in survival of Sphaeroceridae eggs on dung treated with different concentrations of Neporex at medium applications.

Table A8.7: Analysis of variance of the survival of Sphaeroceridae eggs on dung treated with different concentrations of Neporex at high applications.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	1540	5	308	4.98305085	0.00143671	2.47716514
Error	2225.14286	36	61.8095238			
Total	3765.14286	41				

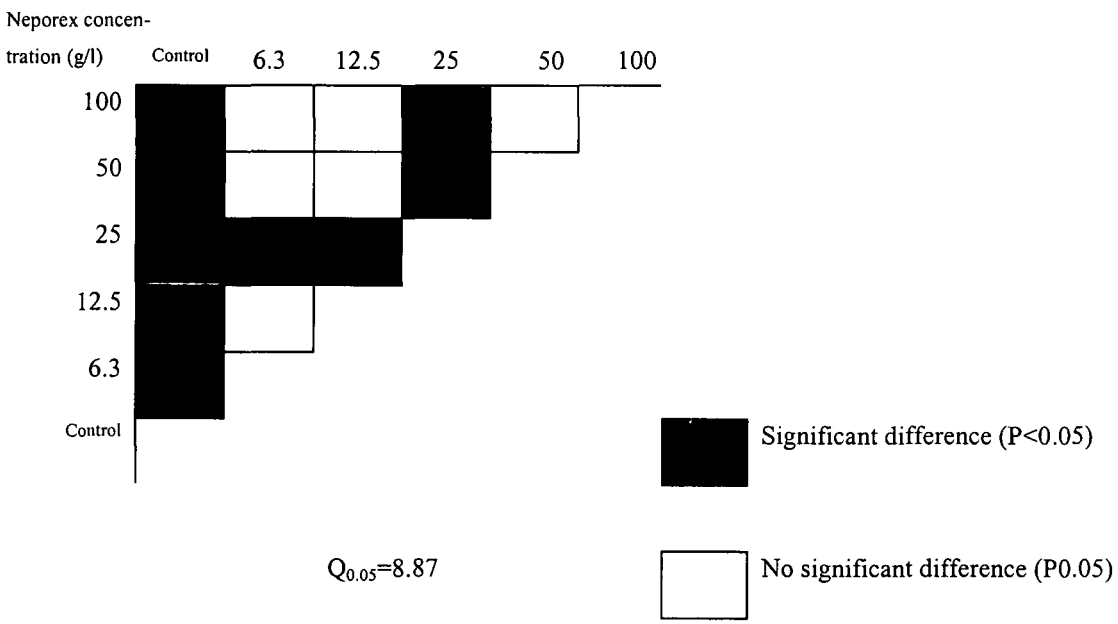


Figure A8.7: A schematic presentation of the significant differences in survival of Sphaeroceridae eggs on dung treated with different concentrations of Neporex at high applications.

Table A8.8: Analysis of variance of the survival of Sphaeroceridae larvae on dung treated with different concentrations of Neporex at low applications.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	21495.2593	5	4299.05185	42.8813299	1.4071E-16	2.4085125
Error	4812.22222	48	100.25463			
Total	26307.4815	53				

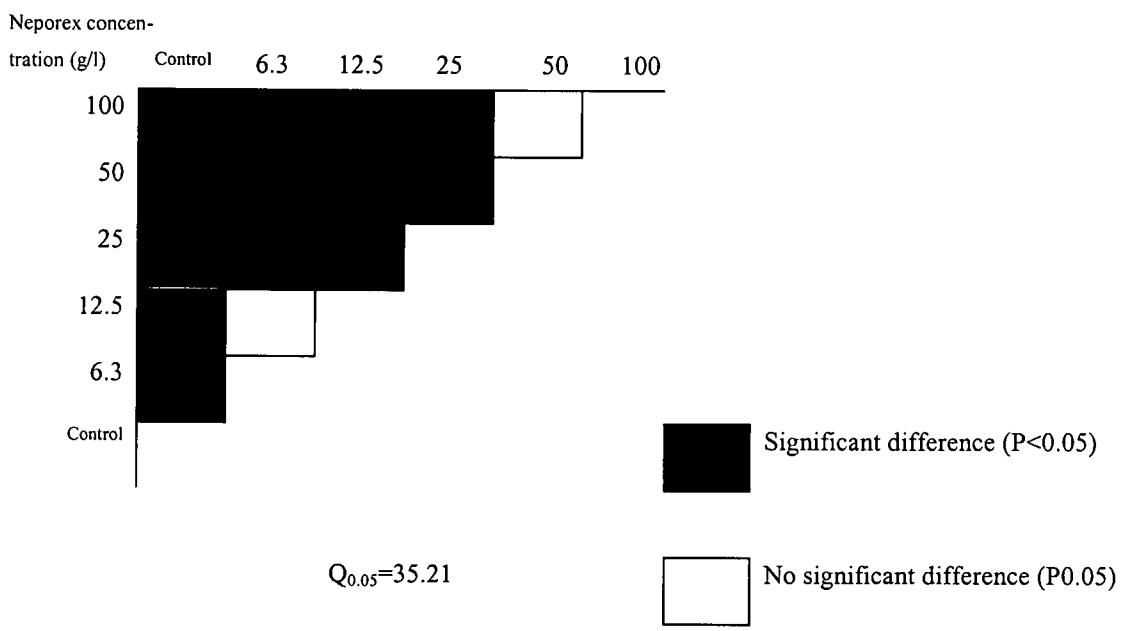


Figure A8.8: A schematic presentation of the significant differences in survival of Sphaeroceridae larvae on dung treated with different concentrations of Neporex at low applications.

Table A8.9: Analysis of variance of the survival of Sphaeroceridae larvae on dung treated with different concentrations of Neporex at medium applications.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	19802.0926	5	3960.41852	35.104042	6.2447E-15	2.4085125
Error	5415.33333	48	112.819444			
Total	25217.4259	53				

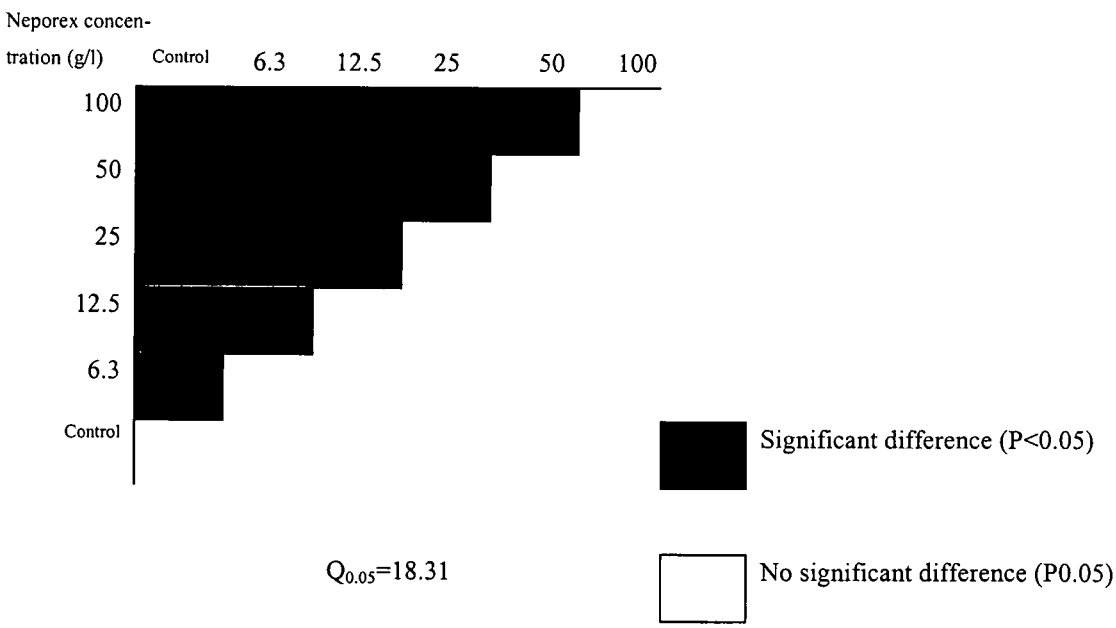


Figure A8.9: A schematic presentation of the significant differences in survival of Sphaeroceridae larvae on dung treated with different concentrations of Neporex at medium applications.

Table A8.10: Analysis of variance of the survival of Sphaeroceridae larvae on dung treated with different concentrations of Neporex at high applications.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	21812.3889	5	4362.47778	53.9348177	1.513E-18	2.4085125
Error	3882.44444	48	80.8842593			
Total	25694.8333	53				

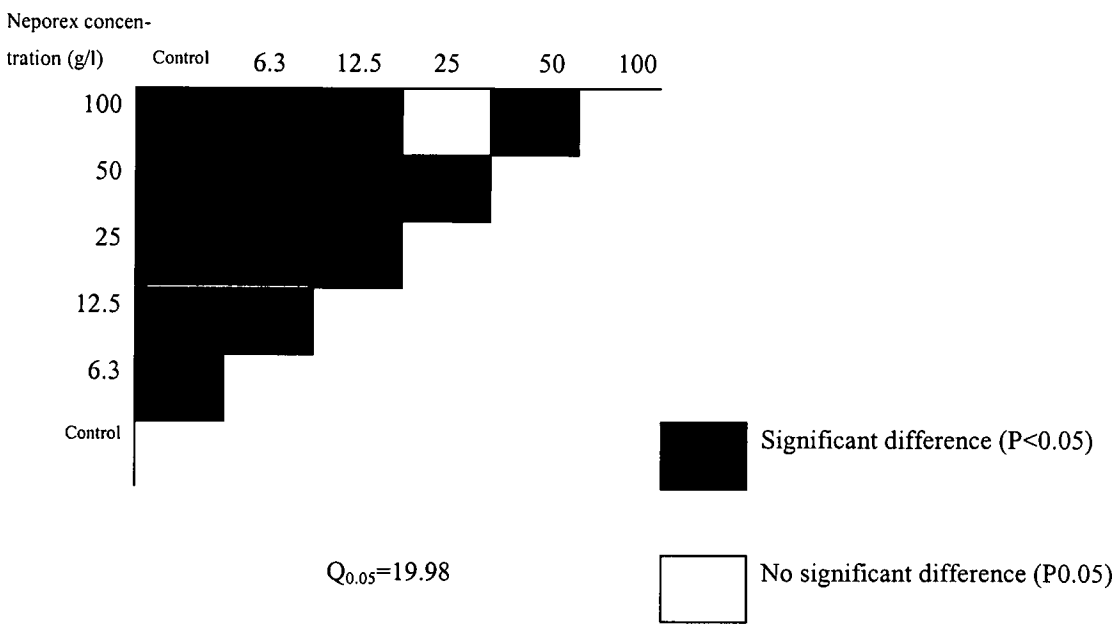


Figure A8.10: A schematic presentation of the significant differences in survival of Sphaeroceridae larvae on dung treated with different concentrations of Neporex at high applications.

Table A8.11: Analysis of variance of the survival of Sphaeroceridae pupae on dung treated with different concentrations of Neporex at low applications.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	12203.1875	5	2440.6375	23.6156717	3.2121E-11	2.43769449
Error	4340.625	42	103.348214			
Total	16543.8125	47				

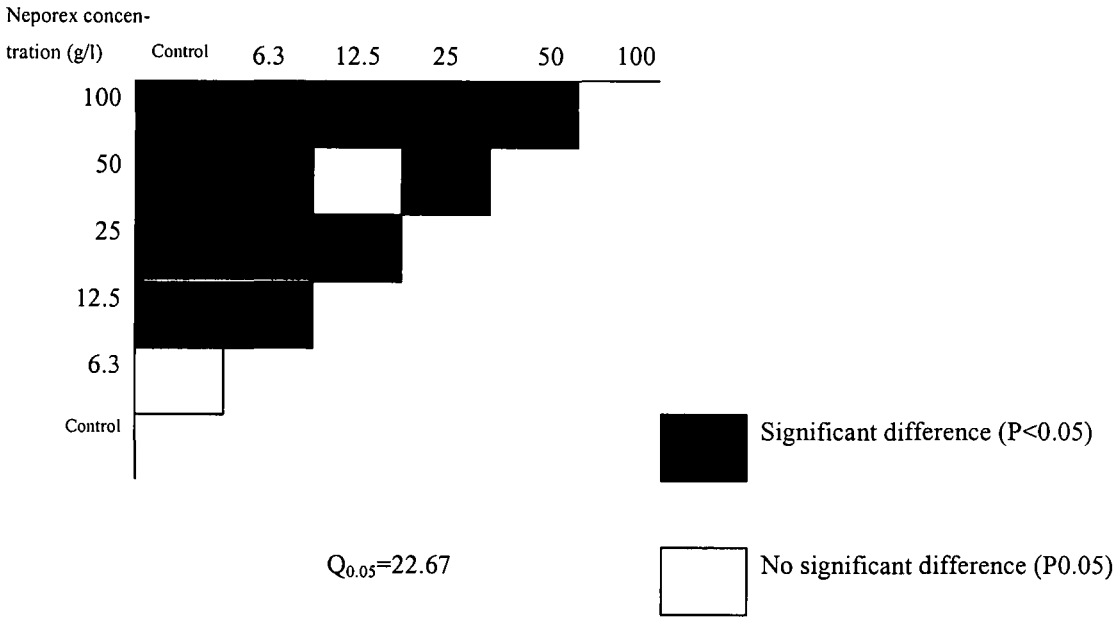


Figure A8.11: A schematic presentation of the significant differences in survival of Sphaeroceridae pupae on dung treated with different concentrations of Neporex at low applications.

Table A8.12: Analysis of variance of the survival of Sphaeroceridae pupae on dung treated with different concentrations of Neporex at medium applications.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	9212.85417	5	1842.57083	41.7946263	3.0198E-15	2.43769449
Error	1851.625	42	44.0863095			
Total	11064.4792	47				

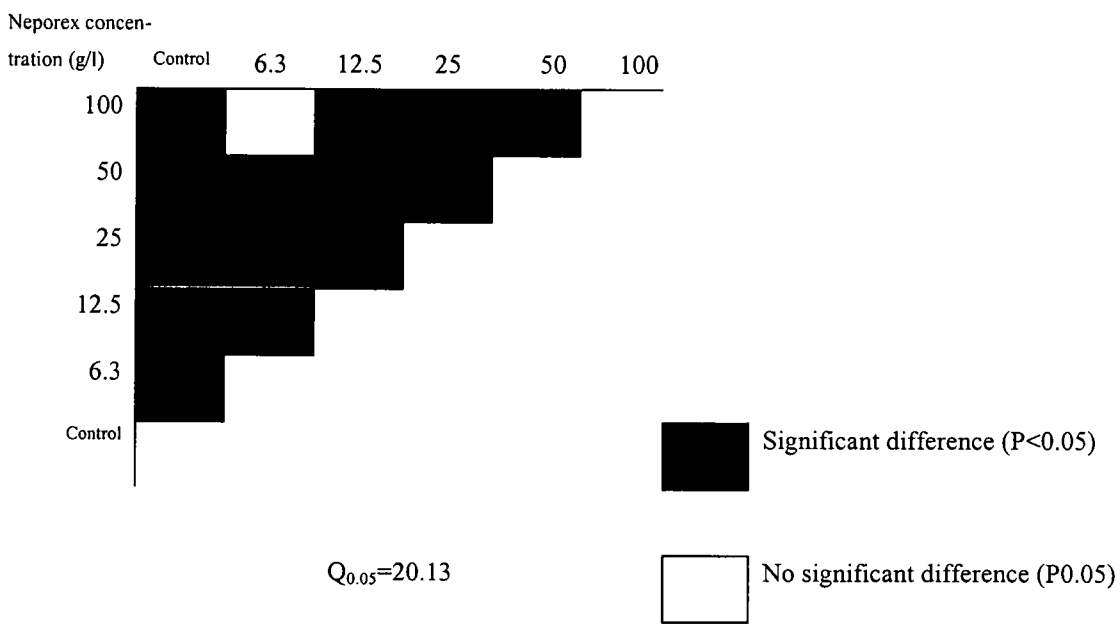


Figure A8.12: A schematic presentation of the significant differences in survival of Sphaeroceridae pupae on dung treated with different concentrations of Neporex at medium applications.

Table A8.13: Analysis of variance of the survival of Sphaeroceridae pupae on dung treated with different concentrations of Neporex at high applications.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	7052	5	1410.4	7.31928459	5.2192E-05	2.43769449
Error	8093.25	42	192.696429			
Total	15145.25	47				

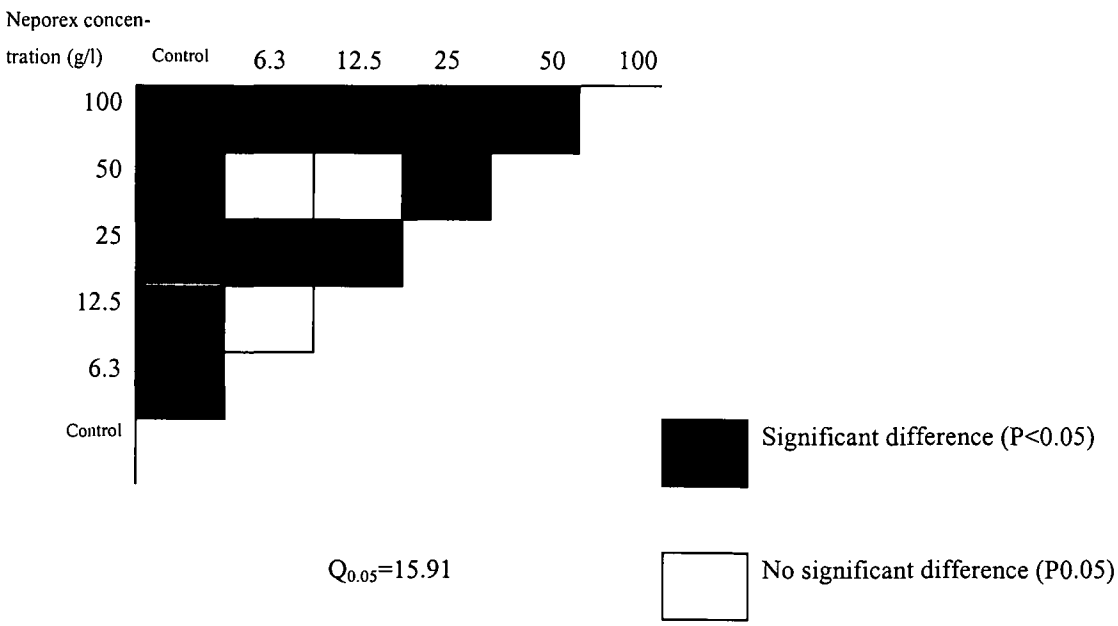


Figure A8.13: A schematic presentation of the significant differences in survival of Sphaeroceridae pupae on dung treated with different concentrations of Neporex at high applications.

Table A8.14: Analysis of variance of the survival of Sphaeroceridae adults on dung treated with different concentrations of Neporex at low applications.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	610.483333	5	122.096667	29.9012245	2.0109E-14	2.38606646
Error	220.5	54	4.08333333			
Total	830.983333	59				

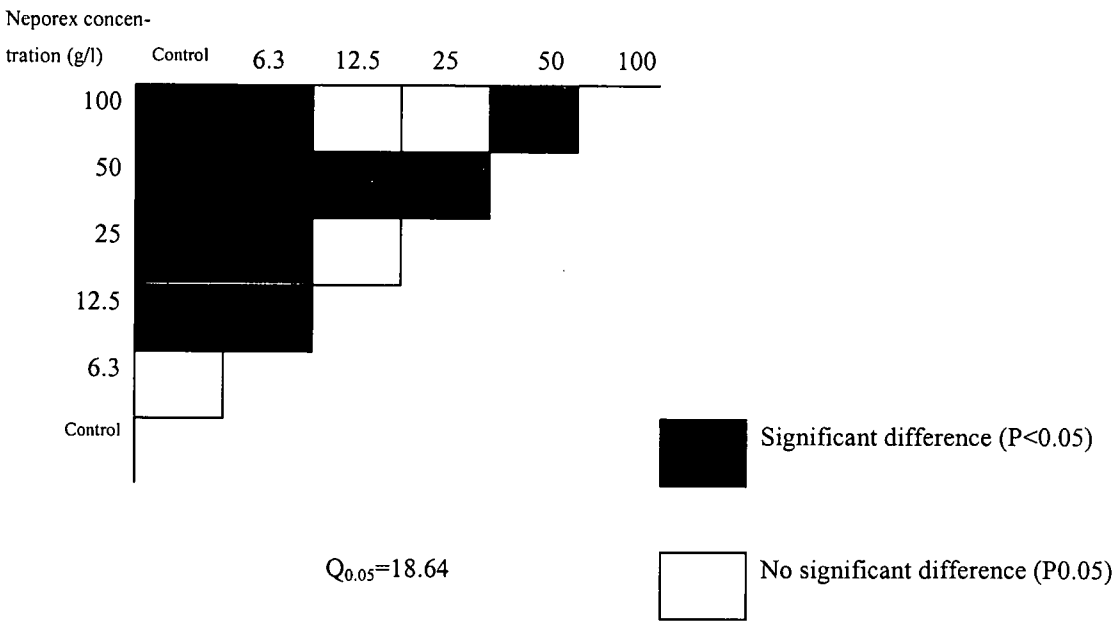


Figure A8.14: A schematic presentation of the significant differences in survival of Sphaeroceridae adult flies on dung treated with different concentrations of Neporex at low applications.

Table A8.15: Analysis of variance of the survival of Sphaeroceridae adults on dung treated with different concentrations of Neporex at medium applications.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	1110.15	5	222.03	80.1981271	9.5993E-24	2.38606646
Error	149.5	54	2.76851852			
Total	1259.65	59				

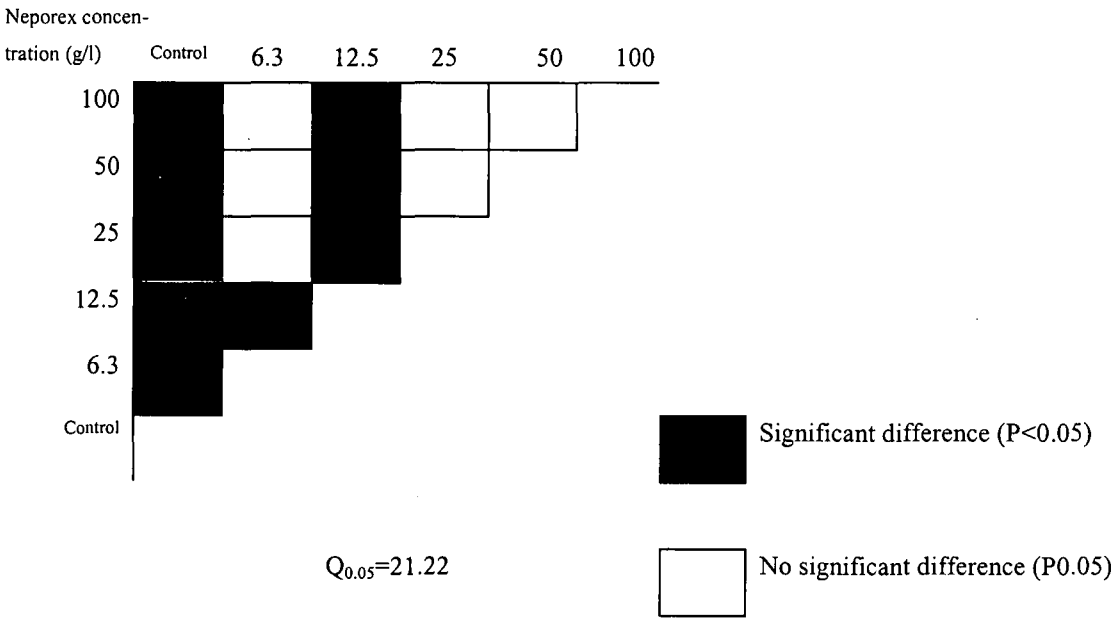


Figure A8.15: A schematic presentation of the significant differences in survival of Sphaeroceridae adult flies on dung treated with different concentrations of Neporex at medium applications.

Table A8.16: Analysis of variance of the survival of Sphaeroceridae adults on dung treated with different concentrations of Neporex at high applications.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Treatments	697.683333	5	139.536667	30.7675786	1.151E-14	2.38606646
Error	244.9	54	4.53518519			
Total	942.583333	59				

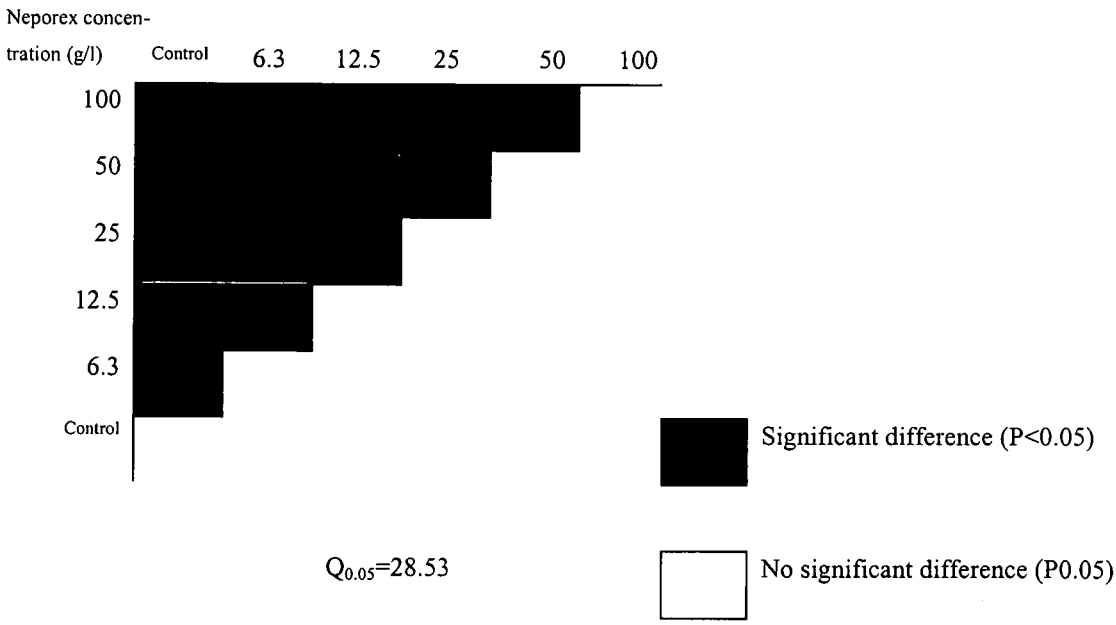


Figure A8.16: A schematic presentation of the significant differences in survival of Sphaeroceridae adult flies on dung treated with different concentrations of Neporex at high applications.

CHAPTER 9

GENERAL DISCUSSION AND CONCLUSIONS

This project was initiated when studies were conducted to determine the seasonal abundance of Sphaeroceridae in the Central Free State was determined. The flies that inhabit undisturbed cattle dung in the field were investigated, but no *C. vagans* or *C. hirtula* species were encountered under these natural conditions. It therefore seems as if these two species are limited to feedlot dung only. Laboratory tests furthermore showed that the composition of feedlot dung had no severe impact on the development and survival of any of immature stages or the adults. This has a major advantage because control measures only need to be taken at the feedlot, since none of the droppings in the field will therefore be affected by these species. In the USA for instance, other pest species like *H. irritans* and *M. autumnalis* utilize natural pats in the field (Poorbaugh, 1966), which further complicate any control measures.

During these succession studies, only five Sphaeroceridae species were encountered, although the conclusion was reached that it is possible for more species to be present on the dung in the area, although none of them would use cattle dung as a breeding medium. They would only visit the pats to feed on the liquid content of the dung.

Temperature studies that were conducted showed that the rate at which adult Sphaeroceridae females was added to the population was zero at the lower critical limit. It was also greatly depressed at temperatures near the limit through the combined effect of low reproduction rates, slow development and high mortality among the development stages. These theoretical temperature limits were estimated by calculating the reciprocal of development time for each of the development stages of both species. Subsequently a steep rise in effective reproduction followed as oviposition rates increased, development speeded up, and mortality of early stages declined. This situation occurred

at temperatures between 24°C and 30°C depending on which development stage or species was referred to. This was followed by a decline as the decrease in longevity of reproducing females failed to be compensated for by further increases in rates of oviposition and development. At still higher temperatures, the life expectations of all stages will fall to zero again, and development velocity decreases. This occurred at temperatures above 36°C for all development stages of both *C. vagans* and *C. hirtula*.

Laboratory colonies of both sphaerocerid species were successfully established. After optimum temperature and moisture conditions for egg production, development and survival of immature stages and adult survival were known typical summer environmental conditions were simulated in the laboratory. This ensured the production of large numbers of healthy sphaerocerid adults destined for further experimental work. These colonies were self-sustainable for the entire duration of the study.

Because Sphaeroceridae species that colonize natural dung pats in the Northern Hemisphere would be subjected to pat degradation, they would therefore only be able to utilize dung pats in the field for a limited period. Conditions at the feedlot are totally different. Because of the large amounts of fresh dung produced by the cattle each day in a very small enclosure, dung is always wet. The entire feedlot can therefore be regarded as one enormous dung pat that is continually kept at optimum moisture conditions. During the summer when temperatures are favourable, Sphaeroceridae flies can therefore continue their life cycle without any chance of pat degradation and their proliferation would not be limited. If the number of eggs that are produced by each female during optimal moisture conditions is taken into account, the numbers of Sphaeroceridae can escalate extremely quickly in only a very short time.

Although sphaerocerids do not feed on blood, fly infestations at feedlots can become extremely heavy at times and as a result of that, the physical condition of cattle deteriorate rapidly. At some feedlots, cattle tend to avoid feeding troughs by day when

flies are a nuisance to them and subsequently overfeed themselves at night when fly activity ceases. Large volumes of fluid are then consumed by the cattle, which can even lead to the death of these animals. The reason why these sphaerocerids are present at feedlots in such large numbers in South Africa and not in any other part of the world is unknown. A few possibilities to this phenomenon exist.

1. These two Sphaeroceridae species (*C. vagans* and *C. hirtula*) were introduced from Europe by sailing ships used for cattle imports during the previous century. Very few predaceous species of larvae are present in feedlot dung in South Africa compared to natural droppings in Europe. The faunal community of droppings in Europe is also very rich (Hammer, 1941; Rohacèk, 1983), and several species of predacious larval Diptera may be present in the same geographical area and presumably in the same pat. On the other hand it was shown that the faunal diversity of feedlot dung in South Africa was extremely poor, and very few predators, except the occasional staphylinid beetle in the drier parts of the feedlot, have been observed. A similar situation exists in Australia, where fly pest species such as *H. irritans* and *Musca vettustisima* Walker are of great economic importance. In Europe, these species are generally not as numerous (Hammer, 1941) as in Australia where fewer other insects inhabit ruminant droppings (Bornemissya, 1960).

2. Management practices at feedlots favour Sphaeroceridae success, but at the same time inimical to the occurrence of natural enemies. These practices include the diet of the cattle that produces dung which is very rich in nitrogen and low in pH, coupled to the irregular removal of dung from the feedlot. The feedlot area was also cleared of all vegetation, and the presence of indigenous trees, hedge rows or tall grass inside the feedlot area could have increased the number of natural predators to the feedlot which could in turn have contributed to keep pest Sphaeroceridae populations below the economic threshold.

3. There is also very little competition for food and space in feedlot dung between the two species of Sphaeroceridae. Laboratory studies indicated that as far as temperature and humidity are concerned, these flies are typically summer species. Environmental conditions at South African feedlots are therefore optimal for the survival and development of Sphaeroceridae larvae and adults and as a result of that, their proliferation during the wet summer months is unlimited.

The success rate of biological and chemical control experiments in the laboratory differed. Biological control agents that were used all failed to bring about a substantial reduction in Sphaeroceridae numbers, even though decreases in Sphaeroceridae numbers were significant in many instances. The conclusion was furthermore made that the majority of the biological control agents used in these experiments were unable to survive in feedlot dung for extensive periods and would therefore not be a viable option.

Chemical control with several bacterial and chemical substances (including Scatterkill and Neporex) was subsequently investigated. These two insecticides proved to be successful both in the laboratory and at the feedlot. However, it was concluded that Scatterkill be used as a chemical control agent because of the effective control it provided against both Sphaeroceridae larvae and adults and also because of the residual effect of Scatterkill in the dung for extensive periods.

The Sphaeroceridae population outbreaks that occurred at Blokhuis feedlot could largely be attributed to unhygienic conditions inside the feedlot camps. Although dung cleanup operations are admittedly labour intensive and expensive, owners will have to realise that effective control of these flies will inevitably cost money. Chemical control provides an alternative, but this will also come at a price. Proper drainage inside the camps is vital during the summer when rainfall is higher to prevent the dung from becoming too moist and contribute further to the successful development and survival

of Sphaeroceridae. If chemical control is implemented, areas around the feeding- and water throughs where most of the dung accumulates and where the Sphaeroceridae are most abundant must be treated thoroughly to provide effective control of the flies.

CHAPTER 10

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PERSONAL COMMUNICATIONS

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SUMMARY

Sphaeroceridae are generally known as "lesser dung flies". These are small to medium sized dark-brown to blackish flies ranging from about 0.5 mm to 6 mm in length. They are saprophagous and occur throughout the tropical and subtropical regions of the world. A unique scenario involving Sphaeroceridae flies that constitute a serious problem at South African feedlots is discussed. Two species, namely *Coproica vagans* (Haliday) and *Coproica hirtula* (Rondani) are both associated with cattle dung at feedlots, with the former species reflecting dominance. The flies cause a nuisance to the cattle by forming black clouds of swarming flies. It therefore became imperative to find a way to control these flies. The establishment of separate sphaerocerid laboratory colonies from which experimental studies could be conducted was successful and is described.

The seasonal occurrence and relative abundance of the Diptera fauna occurring within undisturbed cattle droppings exposed to shaded and sunny locations in the central Free State was investigated. The Sphaeroceridae was of particular interest, but only five presumably new species were discovered among the 21 fly species reared from these droppings. No *C. vagans* or *C. hirtula* specimens were encountered.

The influence of physical parameters such as temperature and moisture content of the dung on the development and survival of immature stages and adult flies is described. Temperature had a major effect on all stages of both species, and both too low and too high temperatures led to severe mortality. Optimum developmental temperatures were between 24°C and 30°C. The development time of all stages also increased with a decrease in temperature. Moisture content of the dung had the same influence on all stages of the Sphaeroceridae, and optimum moisture content levels were at approximately 90%. Development times also increased somewhat with a decrease in moisture content levels of the dung. Oviposition by adult females of both sphaerocerid

species and the influence of temperature and photo periodicy was determined and is described. Oviposition continued for more than 60 days at colder temperatures, although the number of eggs produced was often very low. Higher temperatures on the other hand resulted in large numbers of eggs produced by sphaerocerid females (up to 607 eggs per female) at 24°C, but the duration of oviposition dropped. Different photoperiods had no severe effect on oviposition or egg production. Development and survival of immature stages and adult Sphaeroceridae were also influenced by the type of dung which they were offered and the effect of this phenomenon on the flies is also described. Some dung types, *e.g.* horse, buffalo and rhino dung, had a negative influence on larval and adult survival most probably as a result of the higher fiber contents of these dung types. The other dung types such as cattle, sheep and elephant dung, led to successful development and survival of all stages.

Biological control was attempted with several Coleoptera (a staphylinid, *Philonthus caffer* (Boheman) and scarabaeids *Aphodius pseudolividus* Balthasar and *Harmogaster strydomi* Endrödi), Diptera (*Musca xanthomelas* Wiedemann and *Coboldia fuscipes* (Meigen)) and mite species. These biological control agents all failed to control Sphaeroceridae numbers mainly because of their inability to survive in wet feedlot dung. Chemical control on the other hand produced positive results and seemed like the only option available. Several insecticides and chemicals were tested but only two, namely Neporex (cyromazine) and Scatterkill (piperonyl butoxide), showed irradication potential. A further advantage of Scatterkill is its long residual effect in feedlot dung.

OPSOMMING

Sphaeroceridae staan in die algemeen bekend as "klein misvliegies". Hulle is klein tot medium grootte donkerbruin tot swart vlieë wat wissel van 0.5 mm tot 6 mm in lengte. Hulle is saprofagies en kom meestal in die tropies en subtropiese gedeeltes van die wêreld voor. 'n Unieke aangeleentheid met betrekking tot Sphaeroceridae vlieë wat 'n ernstige probeem inhou by Suid-Afrikaanse voerkrale is bespreek. Twee spesies, naamlik *Coproica vagans* (Haliday) en *Coproica hirtula* (Rondani) word beide met beesmis by voerkrale geassosieer, waar die eersgenoemde spesie dominant was. Die Sphaeroceridae veroorsaak 'n irritasie vir die beeste deurdat hulle 'n swart wolk van vlieë vorm. Daarom was dit uiters noodsaaklik om die vlieë uit te roei. Die vestiging van afsonderlike Sphaeroceridae laboratorium kolonies waarmee eksperimentele studies uitgevoer kon word was suksesvol en word ook beskryf.

Ondersoek is ingestel na die seisonale voorkoms en relatiewe volopheid van die Diptera fauna wat in beesmis voorkom wat aan skadu en son gebiede in die sentrale Vrystaat blootgestel was. Die Sphaeroceridae was van besondere belang, maar ongelukkig was net vyf vermoedelik nuwe spesies ontdek uit die 21 vlieg spesies wat uit die mis gebroei het. Geen *C. vagans* of *C. hirtula* is hier teëgekom nie.

Die invloed van fisiese parameters soos temperatuur en voginhoud van die mis op die ontwikkeling en oorlewing van onvolwasse stadia en volwasse vlieë is beskryf. Temperatuur het 'n groot invloed op all stadia van beide spesies gehad, en beide te lae en te hoë temperature het tot hoë mortaliteite gelei. Optimum ontwikkelingstemperature was tussen 24°C en 30°C. Ontwikkelingstye van alle stadia het ook verhoog met 'n afname in temperatuur. Voginhoud van die mis het dieselfde invloed op alle stadia van die Sphaeroceridae gehad, met optimum voginhoud vlakke van ongeveer 90%. Ontwikkelingstye het ook effens toegeneem met 'n daling in

voginhoud vlakke van die mis. Eierlegging van volwasse vlieë van beide Sphaeroceridae spesies en die invloed van temperatuur en fotoperiode daarop was bepaal en is ook beskryf. Eierlegging het vir langer as 60 dae by kouer temperature geduur, alhoewel die getal eiers wat soms baie laag was. Hoër temperature het aan die ander kant daartoe gelei dat groot getalle eiers geproduseer is deur Sphaeroceridae wyfies (tot soveel as 607) by 24°C geproduseer is, maar die duur van die eierleggingsperiode het gedaal. Verskillende fotoperiodes het geen ernstige effek op eierlegging gehad nie. Ontwikkeling en oorlewing van onvolwasse stadia en volwasse Sphaeroceridae was ook deur die tipe mis wat die vlieë ontvang het beïnvloed en die effek wat hierdie verskynsel op die vlieë gehad het is ook beskryf. Sommige missoorte, soos *bv.* Die van perde, buffels en renosters het 'n negatiewe invloed op die larwes en volwassens se oorlewing gehad, heel waarskynlik as gevolg van die hoër veselinhoud wat hierdie mistipes gehad het. Ander missoorte soos bees-, skaap- en olifantmis tot suksesvolle ontwikkeling en oorlewing van alle stadia gelei het.

Biologiese beheer was met verskeie Coleoptera ('n Staphylinidae kewer, *Philonthus caffer* (Boheman), en twee Scarabaeidae kewers, *Aphodius pseudolividus* Balthasar en *Harmogaster strydomi* Endrödi), Diptera (*Musca xanthomelas* Wiedemann en *Coboldia fuscipes* (Meigen)) en myt spesies probeer. Hierdie biologiese agente het nie een daarin geslaag om Sphaeroceridae getalle te beheer nie, hoofsaaklik as gevlog van hul onvermoë om in nat voerkraalmis te oorleef. Chemiese beheer, aan die ander kant, het positiewe resultate opgelewer en dit blyk die enigste oplossing te wees. Verskeie insektisiede en chemikalieë was getoets maar slegs twee, naamlik Neporex cyromazine) and Scatterkill (piperonyl butoksied), het potentiaal getoon sover dit die uitroei van vlieë betref. 'n Verdere voordeel van Scatterkill was die lang tydperk wat dit aktief in die voerkraalmis gebly het.