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DECOMPOSITION AND ARTHROPOD SUCCESSION ON ABOVE GROUND PIG CARRION IN RURAL MANITOBA.

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DECOMPOSITION AND ARTHROPOD SUCCESSION ON ABOVE GROUND PIG CARRION IN RURAL MANITOBA

A Report for Submission to the Canadian Police Research Centre

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ABSTRACT

This study was conducted to determine the succession of necrophilous insects on sun- and shade-exposed pig carrion. Twenty-two, seventy kilogram, clothed, fresh domestic pig carcasses (*Sus scrofa* L.) were monitored throughout decomposition in three rural areas in Manitoba during trials beginning in spring, summer and fall. A minimum of 13 arthropod orders, 61 families and 95 species collected manually and in pitfall traps over the duration of the study were identified. From this information, the arrival times and duration of stay were recorded for some of the most numerous species: *Calliphora vicina* Robineau-Desvoidy, *Calliphora vomitoria* (Linnaeus), *Cynomya cadaverina* (Robineau-Desvoidy), *Lucilia illustris* (Meigen), *Phormia regina* (Meigen) and *Protophormia terraenovae* (Roboneau-Desvoidy) (Calliphoridae); *Prochyliza xanthostoma* Walker, *Stearibia nigriceps* (Meigen) (Piophilidae); *Necrodes surinamensis* (Fabricius) and *Oiceoptoma noveboracensis* (Forster) (Silphidae); *Creophilus maxillosus* (Linnaeus) and *Ontholestes cingulatus* (Gravenhorst) (Staphylinidae); *Necrobia rufipes* (DeGeer) and *Necrobia violacea* (Linnaeus) (Cleridae); *Glischrochilus quadrisignatus* (Say) and *Nitidula ziczac* Say (Nitidulidae); *Dermestes ater* DeGeer, *Dermestes fasciatus* LeConte, *Dermestes lardarius* Linnaeus (Dermestidae); *Trox unistriatus* Beauvois (Trogidae); *Geotrupes semiopacus* Jekel (Geotrupidae) over the entire decay process. The Calliphoridae predominated in the carcasses during the fresh, bloat and decay stages of decomposition; predators such as the Staphylinidae and some Silphidae arrived in this sequence to feed on these species; as decay progressed, species of Silphidae, Piophilidae, Cleridae, Nitidulidae and Dermestidae, colonized the carcasses. There was no difference in the arthropod community collected

from sun- and shade- exposed pig carrion; however, there were differences in species composition among the three rural areas. *Calliphora vicina* was present exclusively on sun-exposed carrion during the summer trial and on shade-exposed carrion in the spring trial; *Calliphora vomitoria* was collected solely during the fall trial; *C. cadaverina* was found only during the spring trial. *Phormia regina* was the predominant calliphorid species and was present in sun and shade-exposed carrion in all three trials; *L. illustris* and *P. terraenovae* also occurred in all three areas. Ambient air temperature had no observed effect on maggot mass temperature; however, during the summer trial, development time for *P. regina* was faster in sun-exposed carrion. Decomposition and insect colonization were monitored for more than 11 months for the spring trial, 14 months for the summer trial and 12 months for the fall trial. The fresh, bloat, decay and advanced decay stages of decomposition were obvious; however, a discrete stage beyond the advanced decay stage was not apparent. This study provides baseline information on the necrophilous fauna for estimating postmortem interval in cases of human death in Manitoba.

TABLE OF CONTENTS

LIST OF FIGURES

FIGURE

LIST OF TABLES

TABLE

LIST OFAPPENDICES

APPENDIX

CHAPTER 1
INTRODUCTION

Forensic entomology refers to insects and related arthropods and their association with any legal matter. Forensic entomology is divided into three categories: urban, stored product and medicolegal (Catts and Goff 1992; Hall 1990). Urban forensic entomology includes civil law actions and litigations involving arthropods in houses. Stored product forensic entomology includes arthropod infestation of edible commodities. Medicolegal forensic entomology includes arthropod association with felonies such as murder, suicide and rape. In its most practical form, information dealing with carrion insect ecology has been used to estimate the minimum elapsed time since death in homicide cases.

Insects are the primary fauna associated with carrion (Goff and Odom 1987; Payne 1965; Tantawi *et al*.1996). It is known that there is an assemblage of insect species that are attracted to decomposing animal remains and play an active role in the decay process (Anderson and Cervenka 2001; Lord 1990). Certain species in the orders Diptera and Coleoptera represent the majority of the total necrophagous fauna found on carrion (Greenberg 1991; Payne 1965).

Many of these insects have been classified according to their ecological role in carcass decomposition. Typically, carrion is rapidly invaded first by necrophagous flies in the families Calliphoridae, Sarcophagidae and Muscidae. This results in the presence of huge numbers of fly eggs and larvae, thereby providing an abundant food supply for predacious beetles such as silphids, staphylinids and histerids. As the carcass decomposes and food resources become depleted, it becomes attractive to

different insect species for feeding and reproduction. Species in the families Piophilidae, Cleridae and Nitidulidae are typically associated with the carcass during the later stages of decay and the Dermestidae are attracted to the dry remains (Payne and King 1970; Smith 1986; Tantawi *et al*. 1996). Since many of these carrion insects are attracted during these different stages of decomposition, it has been shown that carrion is invaded by certain insect species in a typical sequence or succession (Anderson and VanLaerhoven 1996; Bourel *et al*. 1999; De Souza and Linhares 1997; Early and Goff 1986; Goff and Flynn 1991; Haskell *et al*. 1989; Lord and Burger 1984; Louw and van der Linde 1993; Payne 1965; Tantawi *et al*. 1996; Tullis and Goff 1987).

Many factors can affect insect succession and the decomposition of carrion. Factors such as temperature, season, time of day, accessibility and physical position of a carcass, size and type of carcass, vertebrate scavengers, insect abundance and the biology and geographical distribution of the necrophagous insects can influence the time of arrival and the duration of stay of insects on the carrion (Anderson 2000b; Dillon 1997; Hall and Doisy 1993; Payne 1965; Tessmer and Meek 1996; Tullis and Goff 1987; Williams and Richardson 1984). These many factors make it necessary to study insect succession on carrion in different regions and under different conditions. Generalizations can be made regarding these factors in estimating time of death; however, it leaves open to the possibility of erroneous conclusions that are detrimental to legal cases involving murder and other serious crimes.

It is only within the last twenty years that entomology has been widely used in homicide cases in North America (Hall 1990). The increased interest in forensic entomology has resulted in many studies that have been useful and informative with

respect to the development of insect species lists in certain parts of the world (Aspoas 1994; Baumgartner and Greenberg 1985; De Souza and Linhares 1997; Goff 1992; Hall and Doisy 1993; Introna *et al*. 1991; Wells and Kurahashi 1994). However, many aspects of forensic entomology remain unstudied in many geographical locations.

In North America, studies of this nature have been virtually restricted to the United States. Until the 1970s, there was little forensic entomology data for Canada, which has limited its value as a tool for estimating postmortem intervals in this country (Anderson 2001; Anderson and VanLaerhoven 1996). This has lead to the need for more studies related to insect species composition in different geographical regions throughout Canada and the need to know the resultant factors that influence insect succession and carrion decomposition in different areas. Under the supervision of Dr. Gail S. Anderson at Simon Fraser University, research in forensic entomology in British Columbia has resulted in an extensive and valuable database for this province.

Until recently, the knowledge of insect succession on carrion outside of British Columbia was lacking. Dr. Anderson, therefore, realized the necessity to broaden forensic entomology research, into the other provinces in Canada. Through the funding of the Canadian Police Research Centre and the Manitoba Law Enforcement Services, it was possible to extend this type of research in the province of Manitoba.

For this reason, the main goal of my research was to collect and identify the insect species for part of their life cycle associated with pig carrion in three rural areas in Manitoba. From this information, the timing of arrival and duration of stay of these insects were recorded over the entire decay process of the pig carcasses. Since the succession of insects and the decay of a carcass are influenced by the physical position

and conditions to which the carcass is exposed, pig carcasses were placed in sunny and shaded areas over three different seasons. By accumulating this information about insect succession in selected areas of Manitoba, I have developed a database of forensically important insects. This list will be available for use by law officials for deducing time of death for homicide and poaching cases.

CHAPTER 2
REVIEW OF PERTINENT LITERATURE

CARRION ECOLOGY

Many processes affect the use of carrion by certain species of insects. Micro- and ambient climatic factors, differences in geographic and topographic locations, cues for attraction and competition among species are some of the main influences that affect the succession of insects on carrion. These are key processes in the study of relationships of insects to carrion and to one another (Abell *et al.*1982; Blackith and Blackith 1990; Denno and Cothran 1976; Greenberg 1991; Hall 1948; Tantawi *et al.*1996).

The decomposition process of a carcass can be divided into five main stages: fresh, bloat, decay, advanced decay and dry remains (Tullis and Goff 1987). The arrival and departure of necrophagous insects follow these stages as the breakdown of the carrion proceeds. Each stage is attractive to different species and each stage of decay provides an ideal habitat for certain species to lay eggs and feed. This results in a succession of insect species (Abell *et al.* 1982; Anderson 2000b; Keh 1985; Payne 1965; Turner 1991).

Insects are the primary fauna associated with carrion and are considered most important in recycling this organic material back into the ecosystem. Species in the orders Diptera and Coleoptera are the most important and abundant groups of insects associated with carrion. Certain species in these orders are referred to as necrophagous insects and are responsible for the majority of carrion breakdown. Predators and parasites of the necrophagous insects represent another group of carrion

insects. These species do not necessarily occur in succession, but follow the occurrence of their prey. Other invertebrates occurring on carrion may be adventitious or incidental species. These species occur on and around the carcass and use it only as an extension of their own natural environment. These species are not considered to be successive in occurrence, but some function as secondary predators of the first two groups (Catts and Goff 1992; Keh 1985; Payne 1965; Smith 1986).

Insect colonization of carrion is dependent on many factors. Each geographical region is characterized by its season, temperature, humidity, habitat, vegetation, soil type and environmental conditions (Anderson 2000b; Dillon 1997). These characteristics play a role in influencing insect colonization of carrion. As a result, these defining characteristics of a region influence insect species composition, development times of insects and thus affect the rate of carrion decomposition. For this reason, studies are necessary for different geographical regions. Detailed research regarding carrion insect ecology is necessary to compile accurate lists of carrion insects, to understand the roles they play as decomposers and the times or stages during which they are most dominant during decomposition.

The rate of decomposition of a carcass will be influenced by its exposure to factors such as temperature, rain and wind. Direct sunlight will increase the temperature that the carcass endures, thereby speeding up decomposition, which, in turn, affects insect succession. In open areas, meteorological elements such as wind and rain can create unfavourable conditions for insects that colonize a carcass. In contrast, a shaded area could limit these direct climatic conditions and carrion could, in fact, decay at a faster rate, despite lower temperatures (Early and Goff 1986). It is believed that some

insects, such as calliphorids, exhibit habitat preference and some species are more abundantly associated with one type of habitat than another (Greenberg 1990; Hall 1948).

Decomposition of carrion buried underground is affected by the elimination of major macroclimatic effects, but limits the timing of arrival of carrion insects. Furthermore, many of the insects associated with above ground carrion are restricted from colonizing a buried cadaver (Goff 1992). Carrion submerged in water also leads to changes in the species composition, and thus, the colonization of a carcass (Haskell *et al*. 1989; Vance *et al*. 1995).

FORENSIC ENTOMOLOGY

Forensic entomology, by definition, refers to insects and other arthropods and their association with any legal matter. Most people strictly refer to this term as it is related to the insects or other arthropods associated with a corpse at a murder scene. However, forensic entomology is more accurately divided into three categories: urban, stored product and medicolegal (Catts and Goff 1992; Hall 1990). Urban forensic entomology refers to civil law actions and litigations involving arthropods in houses or dwellings and garden pests, including the misuse of pesticides. Stored product forensic entomology deals with arthropod infestation of commercial stored grain products and other edible commodities, such as chocolate bars and pet foods. The third category is more accurately referred to as medicocriminal forensic entomology and deals with arthropod association with felonies such as murder, suicide and rape. Medicocriminal forensic entomology has also been used in cases involving physical abuse, child

neglect and contraband trafficking (Benecke and Lessig 2001; Catts 1992; Catts and Goff 1992; Hall 1990; Keh 1985; Smith 1986). Fly larvae have also been analyzed to detect drugs and other toxins in decomposing tissue (Introna *et al*. 2001). Much of the research that has been referenced is related to medicocriminal forensic entomology strictly as it deals with questionable death situations. The term, medicocriminal, will therefore be implied and referred to simply as forensic entomology.

Scientists have conducted ecological studies to gather some baseline information necessary to direct the use of carrion insects in more applied areas such as forensic entomology. Research on the effects of temperature on the development of various fly species, geographic differences in fly communities, carrion insect succession on various media, and the effects of various narcotics on fly development have contributed to the applications of forensic entomology (Anderson 2000a; Baumgartner and Greenberg 1985; Blackith and Blackith 1990; Bourel *et al.* 1999; Byrd and Butler 1996; Byrne *et al.* 1995; Cianci and Sheldon 1990; Davies and Ratcliffe 1994; Goff *et al.* 1989; Goff *et al.* 1991a; Goff 1992; Gunatilake and Goff 1989; Introna *et al.* 1990; Johnson and Ringler 1979; Kintz *et al.* 1990a, b; Tantawi *et al.* 1996; Turner and Howard 1992; Wells and Kurahashi 1994; Williams and Richardson 1984). In Europe and the United States, studies of this nature are numerous. In Canada, we are only beginning to see the potential of insects related to their usefulness in forensic entomology.

The first known use of entomology as a forensic tool occurred in the 13th century in China. The suspected weapon used to murder a fellow farmer was a sickle. The investigator ordered all of the land workers in the community to lay their sickles down in front of them. The murderer confessed when fly activity was observed on and around

his sickle (Greenberg 1991; Hall 1990; Smith 1986). Modern use of forensic entomology dates back to 1855, when this technique was first used in a criminal case near Paris, France (Haskell *et al.* 1997). Bergeret is credited with using entomological evidence to clear suspects of the murder of an infant found bricked-up in a fireplace. From 1883 to 1898, J. P. Mégnin, the accredited founder of forensic entomology, published several articles dealing specifically with forensic entomology (Hall 1990). This largely contributed to the awareness among the medical and legal professionals that entomological data could be used in death investigations (Haskell *et al*. 1997). However, others claim that the co-founders of this discipline, Reinhard and Hofmann, used insects and other arthropods as forensic indicators during mass exhumations in Germany and France in the late 1800s (Benecke 2001). Much of this type of research was confined to central Europe for many years (Beneke 2001).

It is only within the last thirty years that entomology has been widely accepted in forensic situations in North America (Anderson 2001; Hall 1990). The increased interest in forensic entomology has resulted in many publications. Bibliographies that contain extensive lists of literature related to this subject have been published (Meek *et al*. 1983; Smith 1986; Vincent *et al.* 1985). These studies are useful and informative with respect to species lists in certain areas. Research on factors such as the effects of season, types of exposure and carcass size and type are common but many aspects of this science remain unstudied. There is a need for more studies related to species composition in different geographical regions and carrion decomposition, under various conditions, throughout North America.

More of these sorts of studies will familiarize officials with the forensic application of entomology and will provide specialized individuals to analyze and interpret this type of data. The demands of forensic entomology require a specialist who is trained in the collection, preservation, rearing and identification of sarcosaprophagous insects. Without the funds necessary to implement these types of studies, the requirements have been difficult to meet, leaving only a select number of people specifically trained in this field. In Canada, for example, Dr. Gail Anderson at Simon Fraser University and her former graduate student, Dr. Sherah VanLaerhoven at the University of Windsor, are the only recognized forensic entomologists for the entire country. Much of the research on sarcosaprophagous insects in Canada is based in various regions of British Columbia, which are very different in terms of topography, climate and insect species composition compared to other provinces. Police officials in British Columbia have been trained through various workshops conducted by Dr. Gail S. Anderson, but exposure to and education in forensic entomology for the rest of the country has been limited.

CARRION AS A HABITAT

Carrion, defined as decomposing animal remains, is a habitat for many arthropods. Carrion is a patchy resource in the landscape. It is an organic addition to the environment that provides a temporary and dynamic food source for a distinct community of organisms such as microorganisms and arthropods (Louw and van der Linde 1993; Tullis and Goff 1987). Carrion is not consistent with respect to its availability as a habitat for insects. Compared to other habitats, carrion is patchy in terms of its

distribution in time and space (Greenberg 1991; Tullis and Goff 1987). Other types of habitats similar to carrion in terms of its distribution in time and space are dung, dead trees and fungi. Many arthropods play a major role in the recycling of this organic matter and are therefore important contributors to the ecosystem.

Insects are the dominant arthropods found on carrion. Payne (1965) reported 522 species of arthropods on pig carcasses, and 85% of these species were insects. Goff and Odom (1987) identified 140 species of arthropods on pig and cat carcasses studied in Hawaii, of which 83% were insects. Tantawi *et al.* (1996) reported that 86% of the total arthropod species found on their pig carcasses in Egypt were insects. Wide varieties of insects are attracted to decomposing remains and play an active role in the decay process (Lord 1990). Carrion flies and beetles are of major importance and use this medium to complete their life cycle. Maggots (fly larvae) are the principle insects and are responsible for the dramatic consumption of carrion tissue (Lord 1990).

CARRION DECOMPOSITION

Decomposition is a continuous process without discrete stages (Schoenly and Reid 1987). However, many researchers have divided this process into four to six stages (Lord and Burger 1984; Payne 1965; Tantawi *et al.* 1996; Turner 1991). The most convenient categorization for carrion decomposition is to divide the process into five stages, namely fresh, bloat, decay, advanced decay and dry remains. The fresh stage begins from the moment of death and ends with the first evidence of bloat. Bloat, or putrefaction, is the most distinctive part of carrion decomposition. Gas production caused from the metabolism of anaerobic bacteria causes the abdomen to expand

(Early and Goff 1986). The internal temperature of the carcass increases drastically during this stage due to the putrefaction process and increased larval fly activity. The decay stage begins when the carcass deflates from perforations in the abdominal wall. The division between the decay and advanced decay stages is dependent on carcass temperature. During the decay stage, there may be huge differences between internal carcass temperature and ambient temperature. As the decay stage finishes, the internal temperature of the carcass begins to match the ambient air temperature more closely (Tullis and Goff 1987). The advanced decay stage begins when most of the muscoid fly larvae have left the carcass. All of the internal organs are reduced to a paste-like or cheesy material. After this matter is consumed and desiccated, the dry remains stage begins. All of these stages vary in length of time and are dependent on factors such as insect abundance and activity, geographic location, temperature, humidity, rainfall, habitat, season and carcass size and type.

Studies to compare carrion available to insects and carrion free from insects have been useful in terms of illustrating the profound effect that insects have on the decomposition process (Abell *et al.* 1982; Payne 1965). Abell *et al.* (1982) studied turtle carrion and compared the effects of decomposition when insects were present and when insects were excluded from the carrion. They found that decomposition of the carcasses was accelerated when insects were present. The turtle carcasses that were caged to exclude insects had evidence of microbial activity but no significant tissue breakdown was observed (Abell *et al.*1982). Payne (1965) conducted a similar study using piglet carcasses. He found that carrion free from insects decomposed very slowly

and retained its form for several months, while the pig carcasses exposed to insect activity were completely desiccated within six days (Payne 1965).

Insect abundance, in addition to other factors such as temperature, humidity, rainfall, habitat and season, are important influences in the rate of carrion decomposition (Tantawi *et al.* 1996; Turner 1991). Furthermore, many of these factors are interrelated. Tantawi *et al.* (1996) showed a direct correlation between the rate of decomposition and temperature. Typically, higher temperatures increase and cold temperatures impede the rates of decomposition. In addition to influencing the rate of decay, temperature also affects the types of insects that arrive at a carcass in a given season. For example, Tantawi *et al.* (1996) reported that *Calliphora vicina* Robineau-Desvoidy was the dominant calliphorid in the winter, while *Phaenicia sericata* (Meigen) bred successfully in carrion in fall, winter and spring, and reached its greatest prevalence in the summer. Since these species have different temperature requirements for development, the rate of decay of the carrion is influenced seasonally. It should be noted that the length of the bloat stage is more dependent on the number of larvae than on temperature (Tantawi *et al.* 1996). High humidity and rainfall also retard the rate of carrion decay. Differences in decomposition were seen in the fall carcasses, probably due to greater rainfall (Tantawi *et al.* 1996). This could have been caused by a decrease in activity of the insect fauna or by a change in the microbial activity within the carcass under wet conditions.

Many researchers in carrion ecology have used different types of animals. Pigs are one of the most common animals used in this kind of research, but rabbits, cats, dogs, mice, birds, turtles and even elephants have also been used to study the decay

process and insect succession on carrion (Abell *et al*. 1982; Blackith and Blackith 1990; Bourel *et al*. 1999; Coe 1978; Denno and Cothran 1976; Payne 1965). The rate of decomposition for these different animals can be affected by details such as accessibility for insects, body hair, feathers, skin type and body size.

Abell *et al.* (1982) showed differences in the pattern of decay on turtle carrion compared to studies in which other vertebrates were used. They suspected that the presence of the shell caused a greater accumulation of liquids, thereby creating a different environment for insects. They viewed this to be the reason for the larger numbers of species in the Drosophilidae and Muscidae that were not found in other studies (Abell *et al.* 1982).

Payne (1965) tried to conduct his carrion study with various animals such as dogs, cats, rabbits, squirrels and birds. He found that acquiring dogs and cats of uniform size was difficult and squirrels and rabbits were difficult to collect. The feathers of the birds created problems in the estimation and sampling of insects (Payne 1965). Except for the Anthropology Research Facility in Tennessee, it is both uncommon and uncustomary to use human cadavers for carrion decomposition and arthropod succession research. Pig carcasses are now commonly used in most carrion ecology and forensic entomology studies. In addition to being readily available, large numbers of pigs can be selected for uniform mass and size. Pigs are relatively hairless, mono-gastric and have a similar skin type to people, making them a reliable model for human decomposition.

The size of a carcass has a profound effect on the rate at which it breaks down and the carrying capacity for fly larvae. Small carrion may offer limited food and affect the survival of the insects feeding and breeding on it (Denno and Cothran 1976; Kuusela and Hanski 1982). Small pieces of carrion and pig carcasses have been used in many studies. Kuusela and Hanski (1982) found that the size of the carrion did not make a difference in the species of flies attracted to the carrion. However, they did observe a positive correlation between the size of the carrion and the numbers of flies bred. It might be expected that a smaller carcass would decompose faster than a larger carcass and smaller carrion or pieces of carrion create a more challenging environment for colonization and development by the fly larvae. This limited food resource results in more intense inter- and intra-specific species competition. As a result, fewer maggots may survive and smaller, stunted larvae may develop. The latter is problematic when using larval size to establish age when estimating a postmortem interval. More research is needed on the effects of carrion size, the resultant competition experienced among carrion insects and the effects these factors have on the decomposition process.

INSECT SUCCESSION ON CARRION

Insects associated with carrion may be classified according to their ecological role. Necrophages feed and breed on the carrion itself. These species typically occur in succession and respond to decompositional changes of the carcass. These species are often the most important in providing useful forensic information. The Calliphoridae are the most prominent necrophages. Sarcophagids, muscids and piophilids may also be necrophagous. Silphids, clerids and dermestids also feed and breed within the

carrion (Catts and Goff 1992; Keh 1985; Payne 1965; Smith 1986). There are also parasites and predators of the necrophagous species. These species are less well understood in terms of their usefulness in forensics, but are nonetheless considered the second most important group that occurs on carrion (Catts and Goff 1992; Payne 1965; Smith 1986). Staphylinids and histerids are important predators of carrion fly larvae and are therefore important in terms of the ecological dynamics of carrion (Tantawi *et al*. 1996). Adventives or incidental species are found in and around the carrion, but only use it as an extension of their own environment. Grasshoppers, crickets, springtails, mites, pillbugs and centipedes fit into this category. It should also be noted that many spiders, centipedes and ants are found in and around carrion and may become incidental predators (Catts and Goff 1992; Keh 1985; Lord 1990; Seastedt *et al*. 1981; Smith 1986). Even though the latter two categories are not considered forensically important, there are over 60 insect families that play an important role in carrion ecology (Smith 1986).

Insect colonization of carrion can be described as a rapid invasion of the carcass by adult calliphorids, sarcophagids and muscids, resulting in the presence of huge numbers of dipteran eggs and larvae. This provides an abundant food supply for predacious beetles such as silphids and staphylinids. Insect diversity reaches a maximum during the fresh, bloat and decay stages of decomposition. As the carcass decays, there is a distinct decrease in species richness. As the food resource becomes depleted, insects disperse from the carcass and different species that prefer the later stages of decay for food and development arrive. Piophilids, clerids and nitidulids are typically associated with the carcass during the advanced decay stage and dermestids

are typically associated with the dry remains stage. This change in species composition on carrion over time is called insect succession. This general pattern has been observed by many scientists and is typical of both temperate and tropical areas (Tantawi *et al.* 1996).

Diptera and Coleoptera comprise about 60% of the total necrophagous fauna found on carrion (Greenberg 1991; Payne 1965). Of the estimated 23 fly and 19 beetle families commonly associated with carrion, there are only about 10 families considered to be worth studying in depth in terms of their forensic value. Among the Diptera, the main families are the Calliphoridae, Sarcophagidae, Muscidae and Piophilidae. Calliphorid larvae, and to a lesser degree, sarcophagids and muscids, are the primary flies responsible for the majority of carrion decomposition during the earlier stages of decomposition (Aspoas 1994; De Jong 1994; Tantawi *et al.* 1996). In the Coleoptera, the main families are the Silphidae, Staphylinidae, Cleridae and Dermestidae and to a lesser degree, geotrupids and trogids (Payne and King 1970). Many of the beetle species associated with carrion are predators of maggots and only a few are true carrion feeders (Smith 1986). However, accounts of the feeding roles of many carrion beetles and other invertebrates are lacking and more research is needed to understand their function during the later stages of decomposition (Kulshrestha and Satpathy 2001).

I. CALLIPHORIDAE

The Calliphoridae is a cosmopolitan group of flies that includes blow flies, green- and bluebottle flies and screwworm flies. Many members of the subfamily Calliphorinae

are necrophagous. When carrion is not available, these insects may feed on dung and other kinds of decomposing refuse (Gillott 1995; Hall 1948).

The life cycle of this family consists of an egg, three larval instars, a prepupa, a pupa and an adult stage. The first two larval instars and the early third instar feed actively on carrion and the later third instar enters a wandering stage. This stage moves away from the food source and searches for a pupation site; however, some individuals may find suitable pupation sites on the carcass. It enters the quiescent stage, called the prepupa, which is characterized by shortening of the body and inactivity. The prepupal stage is followed by the pupal stage, which is characterized by the hardening of the cuticle and formation of the puparium (Morris 1991; Williams and Richardson 1984).

The major influences that affect blow fly establishment and larval development on carrion are competition, carrion size, temperature and humidity (Denno and Cothran 1976; Introna *et al.* 1991). Calliphorids commonly exploit the food resource first, thereby out-competing other fly species. The high fecundity of female calliphorids and rapid larval development create intense competition for food and space for other species, especially on small carrion (Denno and Cothran 1976; Hutton and Wasti 1980; Levot *et al.* 1979; Payne 1965). Denno and Cothran (1976) noted that calliphorid establishment and larval development were initially slowed due to a longer egg development stage compared to other species. They also noted that cooler temperatures at night and low relative humidities resulted in further delays in calliphorid egg development. However, to compensate for this delay, these flies either precede other fly species in the arrival sequence or have faster larval development once

established within the carcass. When food resources are restricted, some calliphorid species have been observed to larviposit, or lay first instar larvae instead of eggs, thereby saving egg development time (Blackith and Blackith 1990; Kamal 1958). This strategy is uncommon; however, it is necessary to take this into consideration when collecting these insects to establish time of death intervals.

According to Hall (1948), *Phormia regina* (Meigen), *Cochliomyia macellaria* (Fabricius) and several species of *Phaenicia* and *Calliphora* are the most important dipteran carrion breeders in the New World. In Manitoba, *Protophormia terraenovae* (Robineau-Desvoidy), *Cynomya cadaverina* (Robineau-Desvoidy), *Phormia regina*, *Phaenicia sericata*, *Lucilia illustris* (Meigen), *Calliphora vomitoria* (Linnaeus), *Calliphora livida* Hall and *Calliphora vicina* are the species typically associated with carrion (Galloway, unpublished data).

Introna *et al.* (1991) conducted a study to determine whether there was a difference in the activity of necrophorous fly species in the spring and summer seasons. *Calliphora livida*, *C. vicina* and *L. illustris* were observed only during the springtime, while *P. sericata* and *Sarcophaga sarracenoides* (Aldrich) were observed only during the summer; a definite seasonal preference of calliphorid species was also described by Hall (1948). Many studies of this type are necessary since the assemblage of carrion flies found on corpses may be determined by their seasonal distribution.

Introna *et al.* (1991) recorded development times for their area since temperature is the critical factor responsible for differences in fly development. They found that decreased nocturnal temperature affected the duration of each immature stage. The pupal stage of most of the species was least affected by differences in

temperature; however, for *P. regina*, there was a significant delay in pupation time at low temperatures. Since this species pupates on the soil surface, it is suspected that this stage is exposed to the same varying ambient temperatures as the larvae.

In Manitoba, *P. terraenovae* and *C. cadaverina* are considered cool weather species and are most abundant in the spring months of April, May and early June. *Phormia regina*, *P. sericata* and *L. illustris* typically emerge in the hot, summer months of late June to August but are also present in low numbers in the later spring months. *Calliphora vomitoria* and *C. vicina* are cool weather species and are typically most abundant in the fall months (Galloway, unpublished data). Species composition in different geographical locations over different seasons, in addition to specific effects of temperature on the insect development, is necessary to evaluate when applying entomological data to estimate time of death (Anderson 2000a; O'Flynn 1983).

II. SARCOPHAGIDAE

The sarcophagids are commonly called flesh flies. Many are scavengers and feed on decaying animal tissue, some are parasites of other invertebrates and a few parasitize vertebrates and are considered primary myiasis producers (Aspoas 1994; Borror *et al*. 1989; Gillott 1995). Carrion can attract several different species of sarcophagids depending on the time of year and geographical area. In Ireland, Blackith and Blackith (1990) collected four species of Sarcophagidae on small corpses such as mice and birds. Denno and Cothran (1976) listed three species of Sarcophagidae breeding in rabbit carrion in California, U.S.A. Introna *et al.* (1991) collected two species of sarcophagids on fresh animal liver in the spring and summer in Maryland,

U.S.A. Tantawi *et al.* (1996) recorded eight species in the spring and summer in Egypt. Aspoas (1994) found seventeen species attracted to carrion-baited traps in South Africa and also found that these flies were most abundant in the summer months. In the warmer temperate and tropical areas, sarcophagids are the primary colonizers of carrion. In the cooler regions, members of this family are considered a secondary invader of carrion compared to the calliphorids (Early and Goff 1986; Payne 1965; Tantawi *et al.* 1996).

Denno and Cothran (1976) found that the life cycle of sarcophagids was generally shorter than that of calliphorids. The feeding larvae of sarcophagids develop more rapidly and in the fall, they pupate and enter diapause. Eclosion occurs in the spring and so they tend to be absent in the winter months in the warmer temperate and tropical regions. Tantawi *et al.* (1996) observed a great abundance of sarcophagids associated with rabbit carrion in spring and fall with a subsequent decrease in the summer. They suspected that some species are not as tolerant of the high temperatures in the summer and there is a resultant decrease in their breeding activity. Denno and Cothran (1976) attributed the small populations of sarcophagids to be the result of competitive pressures with calliphorids. In order to compensate for this pressure, the life history strategy of sarcophagids is geared to the production of a few offspring, which utilize fresh carrion rapidly prior to the exploitation by the calliphorids (Denno and Cothran 1976).

Sarcophagids are limited by their reproductive potential since they deposit many fewer larvae than calliphorids or muscids. However, many sarcophagids are ovoviviparous, which means the females lay first instar larvae on the medium as

opposed to eggs (Gillott 1995). This adaptation may compensate for low fecundity since egg development occurs inside the abdomen of the female. Sarcophagid larvae therefore make immediate use of the carrion for growth and development and are noted to be the first larvae to mature on the carcass (Denno and Cothran 1976). Sarcophagid larvae have also been observed preying on calliphorid larvae and other sarcophagids when carrion size is limited (Blackith and Blackith 1990).

The taxonomy of this group is challenging beyond the family level. Sarcophagids are easily identified to family in the field, but the examination of male genitalia (hypopygia) is the only method for identification to the genus or species level, with exception of one species (Aspoas 1994). Females cannot be identified unless they are gravid and the eggs are reared to produce some adult males for dissection (Aspoas 1994). Although these flies are commonly associated with carrion, their utilization, forensically, is often limited because of the lack of taxonomic expertise and the variability of their presence and abundance on carrion.

III. MUSCIDAE

Muscids are very common flies in a variety of habitats and some are strongly associated with human environments. Species in this family are found breeding and feeding on refuse, excrement and carrion (Smith 1986). Because of their food preference, muscids are more commonly associated with carrion during the decay and post-decay stages, when the internal organs are exposed.

Tullis and Goff (1987) found five species of muscids on pig carcasses during the decay and post-decay stages. These species were dominant during the first half of the decay stage and their numbers decreased with the onset of the post-decay stage.

Muscids were secondary invaders on pig carrion in Brazil, but did not breed in the carcass (De Souza and Linhares 1997). Tantawi *et al.* (1996) found seven muscid species on rabbit carrion and noted that they only bred on the carrion in the cooler seasons.

The forensic importance of this family has not been well documented. Many researchers record their presence and/or abundance, but find this to be too variable to be used as an indicator for time of death.

IV. PIOPHILIDAE

Piophilids are scavengers and some are considered serious pests of cheese and preserved meats (Borror *et al*. 1989). Many larvae also feed and develop in excrement and carrion. *Piophila casei* (L.) is commonly known as the cheese skipper and is named for the jumping movement of the larvae (Smith 1986). This characteristic movement makes it easy to recognize these larvae in the field.

It is the presence of the established larval colonies that is important in terms of the succession of these flies. Adults of *Stearibia nigriceps* Meigen and *Prochyliza xanthostoma* Walker can be found in and around carrion early in the decay process but larval colonization is not evident until the advanced decay stage (personal observation). The larvae feed and develop in the thick, pasty areas of the carcass and are also found in this material near the ground (Tullis and Goff 1987). Since larval piophilids carry out their development during this later stage of decomposition and are the dominant species at this time, they are used as an indicator of time of death.

V. SILPHIDAE

Silphids are commonly found on carrion during the entire decay stage of decomposition and typically remain until the carcass is completely dry (Payne 1965). Larvae and adults commonly feed on maggots; however, the food habits of silphids are not well understood. Some researchers have never observed silphids feeding on carrion, and concluded that they were predacious (Smith 1986). Silphids have been observed feeding on both carrion and larvae and they may only partially be predacious (Payne and King 1970).

VI. STAPHYLINIDAE

Staphylinids are the most common predators on carrion and prey on many insects, but seem to feed heavily on maggots (Smith 1986; Tantawi *et al.* 1996). Payne and King (1970) identified more than fifty species on pig carrion with the first arriving in the early bloat stage and remaining until all insect activity ceased. Both larval and adult staphylinids are predators and many species of larval Aleocharinae are ectoparasites of calliphorid pupae (Payne and King 1970). They also reported that these beetles were active during the day and night and fed on many different insect species; however, they noted that fly larvae seemed to be preferred.

VII. CLERIDAE

Most clerids are predacious in both adult and larval stages. Many are common on tree trunks, logs, flowers and foliage where they prey on various insect larvae (Borror *et al.* 1989). Members of *Necrobia* spp. are scavengers, which is different from the general feeding habits of this family. Adults of *Necrobia* spp. have been observed on

carrion during the decay stage; however, they normally occur on the carcass in the drier stages with the dermestids and nitidulids (Payne and King 1970; Tantawi *et al.* 1996).

Like the other carrion beetles, their feeding role on carrion is uncertain. Tantawi *et al.* (1996) observed that the clerids found on rabbit carcasses showed no signs of predatory behaviour. Payne and King (1970) also observed *Necrobia* spp. feeding solely on carrion, thereby implying that these beetles are true carrion feeders.

VIII. DERMESTIDAE

Dermestids are typically abundant during the dry remains stage of decomposition (Payne and King 1970; Smith 1986). However, Tantawi *et al*. (1996) found these beetles feeding on carrion during the advanced decay stage, after the maggots ceased feeding. They found dermestids to be abundant in the summer, in low abundance in the fall and winter and absent in the spring. The feeding habits of this family are well known. The larvae and adults associated with carrion feed on dried skin, sinews and bones (Payne and King 1970).

IX. NITIDULIDAE

The nitidulids feed on decaying fruit, fermenting tree sap, flowers, fungi and carrion (Borror *et al*. 1989). Payne and King (1970) collected nine species of nitidulids on pig carrion. They observed that the larvae and adults were most abundant during the dry stage of decomposition. Both larvae and adults tend to feed on dried skin but were more commonly seen feeding on the moister areas of the carcass (Payne and King 1970).

X. GEOTRUPIDAE/TROGIDAE

The Geotrupidae are commonly associated with decaying fungi, dung and carrion. Payne and King (1970) observed female geotrupids carrying rolled up balls of carrion into tunnels to be used as food for their young. Typically females bury balls of carrion and dung underground and oviposit into the mass. The larvae feed and develop within the mass (Borror *et al*. 1989). The Trogidae, commonly referred to as skin beetles, are associated with the dried remains of animal carcasses where they feed on dried hide and tissues, feathers or hair. Eggs are laid in the soil beneath the food source and the larvae burrow to the surface to feed (Scholtz 1986). In previous carrion ecology studies, they represented one of the last stages in the succession of insects living in carrion (Borror *et al*. 1989; Payne and King 1970; Scholtz 1986).

FACTORS AFFECTING INSECT SUCCESSION

The effects of geographic distribution, season, temperature, humidity, habitat, and biology of carrion insects influence insect succession (Baumgartner 1988; Baumgartner and Greenberg 1985; Byrd and Butler 1996; Byrne *et al.* 1995; Davies and Ratcliffe 1994; Denno and Cothran 1976; De Souza and Linhares 1997; Goddard 1988; Goff 1991; Greenberg 1990; Grisbaum *et al.* 1995; Hall and Doisy 1993; Hutton and Wasti 1980; Johl and Anderson 1996; Levot *et al.* 1979; Payne 1965; Singh and Greenberg 1994; Tessmer and Meek 1996; Tullis and Goff 1987; Turner and Howard 1992; Vance *et al.* 1995; Wells and Kurahashi 1994; Williams and Richardson 1984). Insects are attracted to an animal immediately after death and detection of the remains can be influenced by these factors (Anderson 2000b; Anderson and VanLaerhoven 1996; Bourel *et al.* 1999; Smith 1986). Immediately following death, biochemical

fermentation processes release compounds such as ammonia (NH_3), hydrogen sulphide (H_2S), carbon dioxide (CO_2) and nitrogen (N_2) (Anderson 2000b; Smith 1986). Necrophagous insects appear in response to these compounds and their activities accelerate the putrefaction process (Smith 1986). Nuorteva (1977) established that blow flies are attracted to carrion in the fresh stage of decomposition but are not attracted to a carcass when it has progressed to the advanced decay stage. This is true in terms of oviposition only, since many adult blow flies are seen visiting the carrion in the later stages of decomposition.

I. GEOGRAPHICAL DISTRIBUTION

Temperature, season and type of habitat define a geographical region and these influence the insect community within that area (Anderson 2000b; Dillon 1997). The species composition in different parts of the world, and even among states and provinces, can be distinctive to that region or overlap across a vast area. For example, in the Old World, species of the genera *Calliphora*, *Lucilia*, and *Chrysomya* are considered the most important carrion species (Smith 1986). In the New World, *P. regina*, *C. macellaria* and species of *Phaenicia* and *Calliphora* are important carrion breeders (Hall 1948). In British Columbia, *L. illustris* was the first species to arrive on pig carrion (Anderson and VanLaerhoven 1996). They reported that this species arrived within minutes of exposure to the carcasses. In contrast, in a similar study conducted in Manitoba, *P. regina* was first to arrive on pig carrion, within minutes of exposure (personal observation).

In northern France, *C. vicina* and *C. vomitoria* were the first species to lay eggs on rabbit carrion (Bourel *et al*. 1999). These species did not arrive until three days after carrion exposure. However, in the following year, *C. vicina* and *C. vomitoria* colonized the carcass within the first day (Bourel *et al.* 1999). In contrast, Tantawi *et al.* (1996) studied the succession of insects in Egypt and found *C. vicina* and *L. sericata* to be the first colonizers on rabbit carrion. There are some generalizations that can be made about the assemblage of species that occur in certain geographic areas. However, studies are necessary within each region, since there are differences in community composition and assumptions could lead to erroneous conclusions pertaining to estimations of time of death (Catts 1992; Lee and Marzuki 1993).

The introduction and dispersal of four Old World *Chrysomya* species into some southern areas of the New World have affected the carrion insect community of these regions (Laurence 1986). This is important in terms of the impact on estimates of time and location of death, since discrepancies between the species composition on a body and the composition of the insect species in that geographical region can provide evidence that a body has been moved (Hall 1990). Regular surveys of blow fly populations must be conducted for regions that could experience introduction of new species to avoid misinterpretations of insect data. Byrne *et al.* (1995) found that the analysis of cuticular hydrocarbons in blow files could be used to provide evidence of corpse relocation. The cuticular hydrocarbons of three geographically different populations of *P. regina* could be distinguished. The implications of this technique are useful for forensic application, but can have misleading results in cases where the site of death and relocation are separated by a short distance (Byrne *et al.* 1995).

II. SEASONAL INFLUENCES

Carrion insects are impacted by season, with specific peaks in activity, abundance and species richness (Anderson 2000b; Smith 1986; Tantawi *et al.* 1996). Calliphorids and sarcophagids exhibit definite seasonal preferences in terms of activity and abundance (Aspoas 1993; Baumgarnter and Greenberg 1985; Bourel *et al.* 1999; Introna *et al.* 1991; Tantawi *et al.* 1996). A corpse exposed in the spring and summer will have a different fauna from one exposed in the late fall or winter, when insect activity has decreased or ceased (Smith 1986).

In Egypt, *C. vicina* was abundant in the winter, *L. sericata* bred successfully in fall, winter and spring and *Chrysomya albiceps* (Wiedemann) was abundant in summer, spring and fall (Tantawi *et al.* 1996). *Phaenicia cuprina* (Wiedemann) was numerous throughout the warm months in the southern United States with peak abundance occurring in the summer (Goddard 1988; Hall 1948). *Cynomya cadaverina* was not abundant during the winter and *P. sericata* numbers peaked in the late spring and early summer (Goddard 1988).

In tropical areas, seasonal influences are related to rainfall and seasons are more appropriately referred to as wet and dry. Differences in species abundance, activity and species richness are also evident in these regions. Baumgartner and Greenberg (1985) found differences in the abundance in species of blow flies during these two seasons in Peru. Abundance of blow flies was greatest in the wet season and least in the dry season. The differences in abundance for this area were also related to altitude and proximity to human habitation.

Seasonal effects that occur within the same area can influence insect abundance. Bourel *et al.* (1999) found a considerable difference in blow fly colonization of rabbit carrion from one year to the next. In 1996, *C. vicina* and *C. vomitoria* were the first species present to colonize the spring-exposed carcasses. However, these species did not arrive until day three and did not lay eggs until day five. In the following year, the activity of these species differed in terms of oviposition. The carrion was exposed during the same time period and *C. vicina* and *C. vomitoria* were seen actively laying eggs on the first day of exposure (Bourel *et al.* 1999). Since there are differences in these generalizations, studies of insect activity and abundance should be conducted throughout a given year and over many years.

The seasonal differences in abundance and activity of blow flies are evident and can be useful in estimating time of death. This is especially useful for corpses found years after death, since blow fly pupal cases and cast beetle skins can be dated to estimate the season of death (Strong and Adams 1990). However, the breakdown and fragmentation of pupal cases and beetle exuviae can be caused from disturbance, sun exposure, moisture, and soil acidity (Anderson 2000b; Nuorteva 1987; Teskey and Turnbull 1979). This technique may not be applicable for all regions that experience extreme weather conditions such as cold winters. Generalizations about seasonality must therefore be applied carefully in forensic situations since many factors can alter this type of evidence (Catts 1992).

III. TEMPERATURE AND HUMIDITY

Temperature and humidity heavily influence insect activity and rates of oviposition and development (Anderson and Cervenka 2001; Gillot 1995; Smith 1986).

This influences the overall rate of decomposition since insect activity is either accelerated or inhibited depending on temperature. Payne (1965) found that the reduction of carrion was slower on cool, cloudy days. The opposite was recorded on warmer days since high temperatures intensified insect activity, resulting in a rapid depletion of the carcass. Therefore, slower decomposition rates and decreased insect activity alter the timing of insect arrival to the carcass, which in turn affects the rate of decay.

Blow flies are typically sensitive to moisture levels. When moisture is too high, blow fly larvae will leave a carcass and have been noted to cease larval development (Payne 1965). Larval silphids and staphylinids have an opposite response to moisture levels and are able to withstand higher moisture levels than blow fly larvae. However, many of these insects will not complete development if the carcass conditions are too dry (Payne 1965; Payne and King 1970).

A combination of microbial metabolism and aggregations of fly larvae can greatly increase temperatures in carrion. These maggot masses and microbial activity create conditions within the carcass that are very different from the surrounding environment. Payne (1965) found that the temperatures of the carcass and air differed by about 16C. Turner and Howard (1992) recorded carcass temperatures of 19-27C above ambient. Carrion temperature has a profound effect on carrion insect development, since the internal temperature of a carcass can be considerably higher than ambient temperature (Catts 1992; Cianci and Sheldon 1990; Goodbrod and Goff 1990; Greenberg 1991; Hanski 1976; Introna *et al.* 1989).

Research on the time spans for species development at different temperatures is key for estimating time of death (Anderson 2000a; Byrd and Butler 1996; Byrd and Allen 2001; Catts and Goff 1992; Smith 1986). Generally, each stage of blow fly development will progress at a slower rate at low temperatures. Davies and Ratcliffe (1994) compared the egg and larval development of *C. alpina* (Zettermann) and *C. vicina* at low temperatures. It was found that *C. vicina* could survive and develop slowly at very low temperatures. They determined that *C. vicina* is important in a forensic context, since postmortem intervals are based on the oldest specimens. Presence of these slow-growing larvae on a body could be misinterpreted since the larvae developing from these eggs will grow faster and appear to be older than the slow growing larvae, therefore altering the estimate of time of death (Davies and Ratcliffe 1994). The microclimate created by maggot masses can also create error in estimating time of death, since the ambient temperature is typically used to estimate the larval growth stage (Turner and Howard 1992).

Ideally, insects should be collected directly from the body at the death scene. In many questionable death situations, collection of entomological evidence is left until after the body has been moved and chilled at the morgue (Johl and Anderson 1996). Research on how refrigeration affects necrophagous fly activity and effects of low temperatures on blow fly development have been necessary to determine whether or not larvae continue to feed and develop on the body during refrigeration (Anderson 2000a; Davies and Ratcliffe 1994; Grisbaum *et al.* 1995; Johl and Anderson 1996). This is problematic since the refrigeration temperatures for body storage may vary and larvae could continue to grow and develop at different rates, therefore influencing the

time of death estimate. *Calliphora vicina* larvae were shown to develop, albeit slowly, at temperatures below 4C and the lag in development seemed to be equal to the length of temperature exposure, with some exceptions (Johl and Anderson 1996). Any lag in development is important to recognize, especially if trying to implicate a murder suspect to a victim. In order to make better forensic inferences, studies on the effects of temperature on the different stages of larval development must be referenced prior to estimating time since death.

IV. HABITAT INFLUENCES

Different habitats can influence carrion species composition and in turn affect insect succession. Tessmer and Meek (1996) noted several differences in species composition of calliphorids on carrion placed in woodland versus pastureland habitats. They found that a greater abundance of blow flies was associated with the pasture habitat. Isiche *et al.* (1992) found a difference in the calliphorid species abundance and diversity when observing mouse carrion in sunny and shaded habitats. Four species were found in the sunny area and only two of these species were observed in the shaded area. Carrion in both habitats contained *C. vicina,* but this species was more abundant in the shaded area. There were also differences in insect succession in different areas of a rainforest habitat where distinct changes in species composition were observed (Early and Goff 1986; Tullis and Goff 1987).

Research on insect succession has been somewhat restricted to terrestrial habitats, and as a result, few studies in aquatic habitats have been performed (Haskell *et al.* 1989; Hobischak and Anderson 1999; Hobischak and Anderson 2002; Johnson

and Ringler 1979; Singh and Greenberg 1994; Vance *et al.* 1995). The successional changes within different habitat types are forensically important. Research is necessary for different habitat types to have data for estimates based on similar conditions, so more confidence can be placed in the inferences made for time of death (Bourel *et al.* 1999).

In many forensic cases, bodies have been buried or disposed of in houses, buildings and in the trunks of cars. This has lead to some questions about the effects of the availability or accessibility of carrion on insect succession. Goff (1991) compared case studies involving remains found outdoors versus indoors and reported significant differences in insect colonization. He suggested that certain fly taxa were restricted to indoor situations and that this information could be used for cases where the body is colonized indoors and then later moved outdoors. It was noted that many of the beetle species were poorly represented in the indoor situations.

V. BIOLOGY OF CARRION INSECTS

Succession is also influenced by the biology of the necrophagous insects. Appetite and reproductive state of adult blow flies can influence whether they are ready to use carrion as a food source or medium for oviposition (Dethier and Bodenstein 1958). Carrion may be available and in ideal condition before the blow flies have finished developing their eggs, therefore causing a delay in arrival or oviposition. Bourel *et al.* (1999) found *C. vicina* and *C. vomitoria* arriving at rabbit carcasses three days after exposure and reported that these flies did not lay eggs until day five. They did not provide any explanation for the delay in arrival or oviposition, but these results differed

from the findings of other researchers who reported calliphorid species arriving at the carcass within minutes of death and eggs laid within an hour of death (Anderson and VanLaerhoven 1996).

Blow flies are usually diurnal in activity and rarely lay eggs at night (Greenberg 1985). Typical daily activity of adult blow flies peaks in the early afternoon and little activity occurs in the early morning and late afternoon (Baumgartner and Greenberg 1985). This is an important detail in forensics cases. From this information, it is assumed that a corpse found at night or in early morning infested with calliphorid eggs or early instar larvae, may have died the previous day or earlier. Greenberg (1990) published evidence contrary to this generalization. He observed nocturnal oviposition of *P. sericata*, *P. regina* and *C. vicina*. He concluded that oviposition is temperature dependent and is not directly influenced by time of day. This is an important observation since the assumption that blow flies rarely oviposit at night can change a postmortem interval by as much as 12 hours (Catts 1992).

Disturbances in blow fly colonization can result from competition between and within fly species. Hutton and Wasti (1980) found that larval competition between *P. sericata* and *P. regina* resulted in a 60% reduction in survival rate for *P. regina*. They established that *P. sericata* was more competitive than *P. regina*, despite abundant food and space. Some fly species have different food requirements that can influence their ability to succeed under certain conditions. *Chrysomya megacephala* (Fabricius), for example, requires less food than other species to develop (Levot *et al.* 1979). This is an important adaptation for carrion flies since many different calliphorid species may arrive at the same carcass at the same time. Competition between different fly families

is also apparent on carrion. Denno and Cothran (1976) recorded calliphorids as the primary invaders of rabbit carrion in California and observed small populations of sarcophagids at the carcasses. They established that when the oviposition of calliphorids was artificially reduced, the numbers of the sarcophagids increased significantly.

There are other factors that can cause a decrease in the arrival time to carrion. Effects of adventive species and vertebrate scavenging, impact the succession of insects on carrion. Fire ants, *Solenopsis geminata* (Fabricius), can have a major impact on necrophagous insects (Early and Goff 1986; Wells and Greenberg 1994). They found that the colonization of carrion, and in turn the rate of decomposition, was retarded when fire ants were in significant numbers. Vertebrate scavengers can intensify oviposition by creating large wounds by feeding and tearing flesh from a carcass. This creates a larger and ideal surface area for fly oviposition since more soft and bloody tissue is exposed. Common vertebrate scavengers are bears, coyotes, wolves, foxes and skunks (Anderson 2000b; Dillon 1997; Nation and Williams 1989). Scavengers can also have the opposite effect and eliminate insect colonization on a carcass. Wolves, for example, can completely devour the carcass tissue and organs, leaving nothing for carrion insects to feed on or breed in (personal observation).

All of the factors that influence the colonization and succession of insects on carrion are important and unique to different regions and can even differ from case to case. Data from one region and assumptions based on past cases should, therefore, be used with caution when determining time of death of a corpse. Studies in different geographical areas and under varied conditions are necessary to generate accurate

insect species lists and arrival times for use in forensic cases. Furthermore, research on the effects of seasonality, temperature and habitat on carrion insect colonization within these regions is important.

FORENSIC ENTOMOLOGY: A TOOL FOR ESTIMATING TIME OF DEATH

Forensic entomology has been useful in estimating the minimal elapsed time between the discovery of a body and the time of death. This is based on the premise that arthropod species colonize carrion, in this case a corpse, in a predictable succession (Hall 1990). Insect evidence from a homicide case is identified, where possible, and analyzed by an entomologist, preferably a forensic entomologist. Depending on influencing factors such as geography, season, temperature and habitat, estimates can be made about the postmortem interval based on the developmental times of the insect species found (Anderson and Cervenka 2001; Catts 1992; Erzinclioglu 1989a; Grassberger and Reiter 2002; Marchenko 1990).

In addition to estimating time of death, forensic entomology has also been used to indicate relocation of a dead body, manner of death and specific sites of trauma on the body (Anderson 1997; Anderson and Cervenka 2001; Lord 1990; Haskell *et al*.1997; Smith 1986). Maggots are also useful in cases where the cause of death is unknown. Bodies of fly larvae can be analyzed for cases involving possible overdoses or poisonings. This procedure is especially important when the body is in the advanced stages of decay. At this stage it is too late to analyze the body fluids and tissues for toxic agents (Gunatilake and Goff 1989; Introna *et al*. 1990; Introna *et al*. 2001; Kintz *et*

al. 1990a, b; Nuorteva and Nuorteva 1982; Pahwa 1991; Patrician and Vaidyanathan 1995).

There have been many case studies where forensic entomology has been a valuable tool for death investigations. See Anderson 1997; Anderson 1999; Anderson and Cervenka 2001; Goff 1991, 1992; Goff and Flynn 1991; Goff and Odom 1987; Goff *et al*. 1991b; Goff *et al*. 1986; Greenberg 1985; Hawley *et al*. 1989; Hobischak and Anderson 1999; Lockwood *et al*. 1994; Lord *et al*. 1992; Lord *et al*. 1986a, b; Mann *et al*. 1990; Nuorteva 1974; Nuorteva 1977; Nuorteva *et al*. 1967; Nuorteva *et al*. 1974; Skinner and Anderson 1991; Teskey and Turnbull 1979 for reviews. However, some of these case studies provided little information as to whether the insect evidence was the key element, or even necessary, in determining time of death. These documented applications of insect evidence have made this technique a legitimate tool for estimating time of death in crime situations. Two specific case histories by Goff *et al*. (1986) and Nuorteva (1974) are described to illustrate the types of reasoning and kinds of inferences drawn from entomological evidence.

Goff *et al.* (1986) related a case of a woman discovered in a brush-filled drainage ditch outside of Honolulu, Hawaii. The mangled remains were in the early post-decay stage of decomposition and partially immersed in water. Collection of the insects associated with the remains occurred during autopsy. The calliphorid larvae were identified from the portions of the body that were immersed in water and a greater variety of insects and empty calliphorid puparia were collected from the drier areas. Additional insect specimens were collected from the site of discovery the following day. From these findings, the authors were able to generate a postmortem interval of 19 to

20 days. This estimate was based on species composition of the insects and the developmental stages present on the remains. This estimate fit with the last confirmed sighting of this woman, which was 20 days prior to the discovery of the body. The insect evidence of primary significance in this estimate was puparia of *Chrysomya rufifacies* (Fabricius) and adult dermestid beeltes, *Dermestes maculatus* DeGeer. These species exhibited the longest period of residence as indicated by the developmental stages collected. It should be noted that knowledge through extensive research of the developmental times of these species and their association with carrion in this region was key in this estimate.

Another interesting case study involved determining the age of a bloodstain in a decaying shirt (Nuorteva 1974). This was considered a very complicated crime involving two murders and a knifing in Finland. The police discovered the bloody shirt wrapped in a plastic bag in a garbage can. This garbage can was located near a house close to the scene of one of the murders. Numerous fly larvae and pupae were on the shirt, which was still wet with decaying blood. The police were unsure how and if this shirt was related to the two murders and the knifing incident. The house where one of the murders occurred was inspected and collections of insects were made. Fly eggs, early instar larvae and older larvae were collected from the shirt. The author suspected that the shirt was colonized twice; once prior to disposal and again in the garbage can. These flies were reared in the laboratory and three fly species were identified. From these data, it was concluded that the fly fauna that emerged from the shirt was similar to the insect fauna recovered from the house, thereby providing police conclusive evidence that the murder occurred in the house.

Forensic entomology has potential to be very informative in human death cases to estimate postmortem interval. However, the way in which this technique is portrayed by the press has been misleading. For instance, in Canada, the media coverage of forensic entomology has neglected to note the factors that complicate its usefulness. As a result, forensic entomology has been glorified and misunderstood. Police officials and other non-experts are, therefore, unable to examine these published 'facts' objectively (Appleby 1992; Blore 1999; Gannon 1997; Snyder Sachs 1998). Most scientists who have published research related to forensic entomology generally mention potential drawbacks associated with these studies and the need for further research and this has been emphasized in some popular articles (McKeowen 1991; Oliwenstein 1988; Royte 1992; Underwood 1990). Unfortunately, these articles are not very accessible to the public or, more importantly, to law enforcement officials who could place false confidence in this approach.

There are many problems in using insect evidence to estimate time of death (Catts 1992). The amount of variability created by the natural environment is enough to make one aware of the difficulties in placing this science in such a high regard without more extensive research. But other problems such as inaccurate insect collection from lack of expertise, lack of taxonomic information, physiological variations of a human corpse and the effects of narcotics on insect development can also result in erroneous estimates of postmortem interval.

Accurate collection and identification of fly larvae can be a problem associated with estimating time of death. In many circumstances the entomologist is not part of the collection team at a homicide scene. It is often necessary to rear live calliphorid larvae

on an artificial food source into later developmental stages for identification (Sherman and Tran 1995). Specific rearing conditions must also be provided in order to collect and interpret developmental data to make more precise estimates of time since death (Anderson 2000a; Grassberger and Reiter 2002). If insect evidence is collected at the crime scene and no live specimens are saved, the entomologist is limited, since identification of many species based on eggs and early instar larvae is difficult, if not impossible (Lord and Burger 1983; Meek et al. 1983). Different preservation and killing solutions, such as ethanol and formalin, have created difficulties in estimating maggot age (Tantawi and Greenberg 1993). A few researchers have published diagnostic descriptions of eggs, larval instars and puparia and alternate techniques for estimating maggot age for forensically important flies (Erzinclioglu 1989b; Greenberg and Singh 1995; Liu and Greenberg 1989; Wells and Lamotte 1995; Westgarth-Smith and Hereward 1989). However, more studies on taxonomy are needed to cover the extensive number of species found on carrion around the world.

Keh (1985) pointed out that two individuals that die at the same time from the same cause could decompose at very different rates, therefore affecting the succession of insects. This is suspected to be a result of the variability of physiological factors, such as amount of body fat or genetic differences of human corpses. As a result, these varied physiological factors have potential to affect estimations of postmortem interval.

Drugs such as cocaine, heroin and methamphetamine can shorten the development time of fly larvae considerably. These differences in the rate of larval development are sufficient to alter estimates of postmortem intervals up to 24 hours for cocaine, up to 29 hours for heroin, and 18 hours for methamphetamine. These

compounds also increase the rate of puparial development (Goff et al. 1991a; Goff et al. 1992; Goff et al. 1989). There was no effect on the development of the actively feeding stages of fly larvae when exposed to a commonly abused tranquilizer in the United States, called phencyclidine. However, differences were observed in the post-feeding stage of development, where the treated colonies developed 3 to 17 hours faster for the remainder of their development compared to the control colonies (Goff et al. 1994).

CONCLUSIONS

Ideally, death investigations require a combined effort of many experts from different disciplines. The forensic entomologist is responsible for the identification of insects and the analysis and interpretation of the entomological data. This information can lead to the determination of the time, cause, manner and place of death supported by the entomological data (Campobasso and Introna 2001; Gaudry *et al*. 2001). At present, many criminal investigators are not trained in the collection, preservation and identification of carrion insects. Unfortunately, a forensic entomologist is not always included in the investigation, because investigators may not realize the value of insects as indicators of minimum time elapsed since death or there is not a certified forensic entomologist readily available to participate (Anderson and Cervenka 2001; Meek *et al.* 1983).

Reliable taxonomic keys are necessary for all instars of maggots and many other necrophagous insects; such keys may not be available. Some research has been done at the biomolecular level to potentially address this problem. The development of DNA-based methods for rapid identification of calliphorid and scarcophagid larvae associated

with carrion has proven helpful (Malgorn and Coquoz 1999; Sperling *et al.* 1994; Stevens and Wall 2001; Wells *et al*. 2001). This technique has potential for the identification of early instar larvae and poorly preserved insect specimens, which are common obstacles in forensic cases. However, this technique is limited since the funding and accessibility to such technology is not always feasible.

At present, there are too many discrepancies and deficient details for forensic entomology to be an indisputable source of evidence in the courtroom. These gaps in the total knowledge of this science put an entomologist at risk in the courtroom as the expert witness (Meek *et al.* 1983; Smith 1986). Without more convincing research related to all factors affecting insect colonization of a corpse, conflicting expert testimony will be common. This is problematic, especially if two forensic entomologists appear in court on behalf of the defence and prosecution and present contradictory interpretations of the insect evidence. Forensic entomology therefore could be judged as an unreliable technique.

Accurate information of the biology and ecology of carrion insects is critical to establish well-substantiated estimates. Data are required from various geographical regions relative to the determination of species composition and associated climatic parameters. Furthermore, additional research is essential to investigate the effects of the factors that influence species composition, insect succession and carrion decomposition (Anderson 2000b; Meek *et al.* 1983).

The role of the entomologist in forensic science is recognized by an increasing number of law enforcement agencies, crime lab services and wildlife departments. The

predictable sequence of insect arrival on carrion has proven to be a useful technique in determining time of death for a variety of cases (Greenberg 1985). However, the value of forensic entomology in criminal investigations has not been fully realized and further research is necessary for this science to be convincing in the rigid, factual place of law.

CHAPTER 3
METHODS AND MATERIALS

STUDY SITES

This research was conducted at three rural sites in Manitoba in order to evaluate the insect fauna associated with pig carrion in sunny and shaded areas. The three rural sites represented three trials, each beginning in a different season (Table 1).

The summer trial was conducted at the Glenlea Research Station (GRS) [49º 38' 08" N; 97º 08' 06" W] owned by the University of Manitoba. The surrounding area was agricultural with crops on either side of the study site. The sunny area was an open field consisting of various grass species. The shaded area was in a windbreak, which consisted of narrowly, planted rows of green ash (*Fraxinus pennsylvanica* Marsh.), Siberian elm (*Ulmus pumila* L.), American elm (*Ulmus americana* L.), willow (*Salix alba* L.), white spruce (*Picea glauca* (Moench) Voss) and scattered cottonwoods (*Populus* sp.) that provided enough canopy cover so that carcasses were not exposed to direct sunlight. This trial began 30 June, 1998. The collection of insects from the carcasses for this trial continued until 01 September, 1999 for a total of 427 days.

The fall trial was conducted in the Sandilands Provincial Forest (SPF) [49º 19' 51" N; 96º 09' 41" W] and began 29 August, 1998. This is a large provincial forest, spanning approximately 3000km^2, with predominantly sandy soil and is covered with a forest of mixed hardwoods, pine and spruce. The sunny area consisted of mainly sparsely planted young jack pine (*Pinus banksiana* Lamb.) trees. The shaded area was a densely planted forest mainly of red pine (*Pinus resinosa* Ait.). Sampling for this trial continued until 31 August, 1999 for a total of 366 days.

The spring trial was conducted on private property in Elm Creek (EC) [49º 40' 32" N; 97º 59' 33" W] and began on 29 May, 1999. The sunny area was an open field consisting mainly of alfalfa. The shaded area was densely forested consisting mainly of deciduous trees, namely green ash and Manitoba maple (*Acer negundo* L.). Sampling for this trial continued until 15 May, 2000 for a total of 351 days.

Each site was selected on the basis of specific criteria. It was necessary for these sites to be easily accessible by vehicle and we also needed sufficient room to distribute the pig carcasses in both sunny and shaded areas. The rural sites were also selected to ensure limited public access to minimize potential human interference, allowing natural insect associations with each carcass. To simulate uniformity among trials, carcasses were placed in open fields with no canopy cover, which constituted the sunny areas. This allowed the decomposing carcasses and associated insect fauna to be exposed to direct sunlight conditions (Figure 1). Similarly, carcasses were placed in forested areas with near full canopy cover, which constituted the shaded areas. This excluded the carcasses and the associated insect fauna from exposure to direct sunlight (Figure 2).

CARCASS TYPE

It is known that pigs (*Sus scrofa* L.) are similar to humans in terms of their digestive process, skin type and the quantity of body hair; it was assumed that a pig carcass would decompose in a similar way as a human cadaver (Catts and Goff 1992). Pigs were used as a model to mimic decomposition of a human cadaver for this study. In order to utilize the information from this study to estimate time of death, it was

necessary to record insect colonization and to study the decomposition of each carcass from as close to the point of death as possible, therefore the day of death of the pigs was recorded as Day 0 (Table 1)

Each pig carcass weighed approximately 70kg and was killed by an electric gunshot to the head by a local farmer. The carcasses were washed and immediately transported from the pig producer's farm to the study site. Each carcass was clothed with pants, shirts and socks because human corpses are often found clothed or wrapped in some kind of cloth material and clothing is known to influence decomposition (Dillon 1997). Each carcass was stabbed in the thorax under the foreleg with a hunting knife with a 10cm blade to simulate a typical homicide wound. The day of death was recorded as Day 0 for each trial. These carcasses were then placed in cages on steel grids placed on the ground.

Carrion is attractive to many vertebrate scavengers such as bears, skunks, wolves, foxes and coyotes. For this reason carcasses were protected in cages made from steel and designed specifically to minimize interference by scavengers. Each cage was 1.22m x 0.76m x 0.76m and was placed within a $34m^2$ plot. Each cage supported a steel hinged lid for easy access to each carcass for sampling and weighing (Figure 3). Based on the scavenger fauna, it was not necessary for the pig carcasses at Elm Creek, MB to be protected in the steel cages, therefore cages constructed from wood and wire mesh (1mm gauge with 5cm inside diameter) were built for this trial (Figures 1 and 2).

SITE SETUP

The distance between each carcass was at least 50m to simulate an isolated resource for insects inhabiting each carcass. Six pig carcasses were placed at Glenlea Research Station, three in the sunny area and three in the shaded area. Eight pig carcasses were placed at each of the Sandilands Provincial Forest and Elm Creek sites, four in the sunny area and four in the shaded area (Figure 4).

Insect data collected from these trials correspond to pig carcasses A, B, C and D for all three locations. There were two control carcasses at Glenlea Research Station (Ec and Fc) and four control carcasses at both Sandilands Provincial Forest and Elm Creek (Ec, Fc, Gc and Hc). Insects were not collected from pig carcasses labeled Ec, Fc, Gc and Hc. These carcasses were used to make descriptive observations without any possible disturbances due to sampling.

INSECT SAMPLING

Carcasses were sampled in order to record the timing of arrival and duration of stay of carrion insects and to compare the insect activity in sunny and shaded areas. During each trial, insects were collected using a battery-powered aspirator, hand-picked using forceps, and by sweep net inside and around the cages (Figure 5). Using these methods, insects were sampled from pig carcasses A, B, C and D every second day at the Glenlea Research Station site for four weeks. Likewise, insects were sampled from pig carcasses A, B, C and D every day at the Sandilands Provincial forest site for two weeks and from pig carcasses A, B, C and D every day at the Elm Creek site for three weeks. Samples were taken less frequently after the period of peak maggot activity for each trial, which was denoted by the dispersal of the maggots away from the carcasses.

All insects were collected into vials of 70% ethanol for preservation and returned to the lab for identification. Samples were sorted and identified to family level first and the carrion insects were subsequently identified to species level. Appendix 1 is an extensive list of all the taxa collected from all three locations. However, due to the enormous numbers of insects collected, only species having recognized forensic relevance were used to assess insect succession on pig carrion over time in sunny versus shaded areas.

It should be noted that relative abundances of insects hand-picked from the pig carrion were based on personal observations taken at the time of sampling.

An extensive voucher collection of the forensically significant insects associated with pig carrion in Manitoba has been submitted for reference in the J. B. Wallis Museum located in the Department of Entomology, University of Manitoba. *Necrodes rufipes* (DeGeer) (F. Cleridae), *Dermestes frischi* Kugelann (F. Dermestidae) and *Acritus nigricornis* (Hoffman), *Margarinotus brunneus* (Fabricius) (F. Histeridae) were reported from Manitoba for the first time.

PITFALL TRAPS

Pitfall traps were used to record the time at which the maggots first entered the wandering stage of development. This sample technique proved to be a useful way to determine when maggots first entered the wandering stage of their development and how long this stage lasted. These traps were also used to record the directional movement of calliphorid larvae. Four proximal pitfall traps surrounded each sampled carcass and were positioned one metre from the cage (Figure 6). These pitfall traps

collected only a portion of the astronomical numbers of maggots associated with each carcass. A distal pitfall trap was placed 15 m from each caged carcass (Figure 6).

Pitfall traps were placed into the soil so the lip of each pitfall container was flush with ground level (Figure 7). Each pitfall trap consisted of two 500ml plastic honey containers (outside diameter = 11.5cm), one inside the other. A saturated salt (NaCl) solution with a drop of detergent was used in each container to drown the insects. Saline solution is a temporary insect preservative and is harmless to animals that might drink from the traps or feed on the trapped, dead insects. A drop of detergent was used in each trap to reduce the surface tension of the saline solution; this ensured that the insects sank to the bottom of the pitfall container. Wooden covers were designed to stand above each pitfall trap to ensure that the traps did not overflow in the event of rain. Insects from each pitfall trap were collected on a weekly basis and strained into a container for preservation and identification. Collection from these traps ceased after the peak period of maggot dispersal was completed.

The original intention of these pitfall traps was to identify all of the taxa captured in each trap. This plan was changed when it was realized that preserving, sorting and identifying the massive numbers of insects collected was impractical due to the time line of this project. An attempt was made with the pitfall traps collected from one sample date from the peak maggot period at Glenlea Research Station. It took an equivalent of one summer season and two people full time to work completely through and identify all the taxa present.

It was necessary to design a sub-sample protocol to estimate the abundance and species richness of maggots trapped in each pitfall trap. Each pitfall sample was

numbered according to its position relative to the carcass and was treated separately in the laboratory. Wet weights of each sample were measured in grams and spread evenly across the bottom of a sampling tray (inside diameter of universe = 32cm x 21.7cm). Three randomly selected sub-samples were collected using a plastic petri-dish with a diameter of 3.6cm. Wet weights of each sub-sample were measured in grams and the numbers of individuals were recorded. The numbers of maggots per gram were calculated and the mean for all three sub-samples was multiplied by the total wet weight of the pitfall sample. Precision was determined from three samples and was always less than 3.0%; therefore no corrections to estimated numbers were made. Each sub-sample of maggots was identified to the species level in order to estimate the proportion of the maggots of each species and the abundance of maggots associated with each pitfall trap.

TEMPERATURE DATA

Since insect activity and carrion decomposition are influenced by temperature, HOBO® temperature data loggers were used to record the ambient and internal carcass temperatures in sunny and shaded areas at all three locations. Temperature data were also collected to determine correlations between air temperature, carcass temperature, maggot masses and stages of decomposition. Internal temperature probes were placed in a knife wound in the thorax of each pig carcass (Figure 8). Ambient air temperature readings were taken at approximately 1m above ground level and positioned adjacent to the distal pitfall traps located 15m away from the carcass (Figure 9). Daily mean temperatures were calculated from hourly data logger recordings.

CARCASS WEIGHTS

Carcasses were weighed in order to compare biomass loss of sunny versus shaded pig carcasses. Carcasses were weighed once per week for the summer and spring trial until no change in mass was detected. No weights were taken for the fall trial. Each carcass was placed on a steel grid on the ground. The steel cages were designed to hold a tripod with a scale (Figure 10). Chains and clamps were attached to the steel tray and then attached to the hook of the scale and tripod. Each carcass was winched above the ground surface so that a free weight could be recorded. The winch was a 1-ton, 5mm diameter cable puller and the scale was a 300lb capacity hanging dial scale.

PHOTOGRAPHS

On each sample day, photographs of each carcass were taken in order to estimate when each stage of decomposition occurred and to determine whether there was a correlation between these stages and insect arrival and duration of stay. From this information, it was determined that certain insect species arrived in a predictable sequence in the decay process of pig carrion in sunny and shaded areas. This was determined by comparing these stages of decay to the insect arrival and duration of stay over time. At least four photographs were taken of each carcass using a Nikon F-50®, 35mm camera. Fuji® slide film was used for best resolution and storage.

Hand written notes were taken on each sample day in order to make generalizations regarding temperature, wind speed, precipitation and cloud cover at the time of sampling. Descriptions of the overall state of the carcasses, general

observations on vertebrate and invertebrate activity and anomalies that had occurred at each site were also recorded.

CHAPTER 4
RESULTS

GLENLEA RESEARCH STATION - SUMMER TRIAL

The summer trial at Glenlea Research Station began on 30 June, 1998 (Day 0). Six pigs were killed, clothed, stabbed and placed in cages. HOBO® temperature data loggers were situated in both sunny and shaded areas to measure internal carcass and ambient air temperatures. On specific sample dates each carcass was weighed, photographed and observed for insect activity. Observations and insect sampling ceased at first frost on 01 October, 1998. Sampling resumed at first thaw after the winter period. This time period will be collectively referred to as the post-winter period (14 May, 1999 to 01 September, 1999).

WEEK I:

Day 0, or the day of death, was the start of the fresh stage of decomposition (Figures 18 and 20A). The mean mass of the carcasses situated in the sunny area was 67kg and of the carcasses placed in the shade, 66kg (Figure 21). The mean ambient air temperature in the shade was recorded at 25.2C and 25.1C in the sun (Figures 22 and 23). The mean internal carcass temperature in the shade was 26.4C and 25.9C in the sun (Figures 22 and 23). The arrival of adult calliphorids and oviposition occurred within 30 minutes of pig placement. It was observed that oviposition occurred sooner on pigs in the shaded area. However, adult calliphorids had colonized and oviposited on all pig carcasses within four hours of pig placement (Figure 19A). From sweep net and hand-picked samples, the dominant calliphorid species in both sun and shade was *Phormia regina* (Meigen). Gravid female *P. regina* were evident in both sun and shade

on Day 0; there was no notable difference in the timing of arrival of this species to the carcasses (Figure 11).

Evidence of the start of the bloat stage began on Day 2 (Figures 18 and 20B). The expanded head and abdominal area and the green colour were clear indications. There was an initial increase to 67.5kg in the mean mass of carcasses in sun and shade due to gas expansion and insect abundance (Figure 21). The mean ambient air temperature in the shade was 20.7C and 23.4C in the sun (Figures 22 and 23). The mean internal carcass temperature in the shade was 22.2C and 24.8C in the sun (Figures 22 and 23). Adult calliphorids were all over the cages, carcasses and in the surrounding grassy area. Calliphorid eggs, early and late first instar larvae extensively covered the head areas. Eggs and larvae were especially concentrated in and around the mouth and nostrils, under the eyelids and behind and inside the ears. Adult blow flies were also laying eggs in the head and chest wounds and within the folds of the clothes (Figure 19B). Early and late first instar larvae were also very numerous in these areas.

Silphids and staphylinids were observed crawling on top of and underneath the carcasses. *Necrodes surinamensis* (Fabricius) (F. Silphidae) was the dominant silphid collected. Adults were observed and collected from the carcasses sooner in the shade (Day 2) than in the sun (Day 6) (Figure 13). This species was collected on Day 2 in the shade only and was consistently present until Day 41 (Figure 13*). Creophilus maxillosus* (Linnaeus) (F. Staphylinidae) was first observed and collected from carcasses in sun and shade on Day 2 (Figure 14). This species was the dominant staphylinid and occurred throughout the first 83 days in the sun and the first 50 days in the shade. This

species was not observed in the shade in the post-winter period. After the winter, adult *C. maxillosus* were collected from pig carcasses in the sun until near the end of the sampling period (Day 342). Adult *Ontholestes cingulatus* (Gravenhorst) (F. Staphylinidae) were observed and collected sooner in the sun (Day 2) than in the shade (Day 15) (Figure 14).

By Day 3, all pig carcasses showed extreme signs of bloat (Figure 20B). Overall, the bloat stage lasted until Day 6 in the sunny area and until Day 8 in the shaded area (Figure 18). Some carcasses were extremely distended, to the point where the pressure was tearing the flesh apart. These areas were subsequently filled with eggs and larvae. From photographs and observations, it was noted that the carcasses in the sunny areas were advancing in the decay process at a faster rate than in the shaded area. Adult calliphorids, eggs, and first and second instar larvae were observed in the mouths, ears, noses and knife wound areas of all of the pigs. The head area was blanketed with maggot activity (Figure 19C). Thousands of eggs and first and second instar larvae were also found in the blood-soaked folds of the clothing. It was also observed that there were more adult calliphorids in the sun than the shade and the numbers of calliphorid eggs were much higher on the shaded carcasses. On Day 3, the mean ambient air temperature was recorded in the shade at 20.2C and 25.1C in the sun (Figures 22 and 23). The mean internal carcass temperatures were logged at 19.8C in the shade and 25.6C in the sun (Figures 22 and 23). On this day, a female *N. surinamensis* was observed ovipositing into the soil underneath the head area of a shaded pig carcass.

By Day 6, the carcasses in the sunny area had deflated and the decay stage began (Figure 18 and 20C, D). The mean carcass mass decreased to 47.5kg in the sun and 53.5kg in the shade (Figure 21). The mean ambient temperature in the sunny area was 21.2C and the internal carcass temperature increased to 29.4C (Figure 22). The shaded carcasses seemed to deflate more gradually and the decay stage for these carcasses was not apparent until Day 8. Mean air temperature of the shaded area was 19.0C and the mean internal carcass temperature increased to 23.2C (Figure 23).

Adult calliphorids were still abundant and the carcasses were literally bubbling with maggot activity (Figure 19D). Thousands of first, second and third instar maggots shrouded each pig carcass. As the result of maggot feeding, the head area of many of the carcasses had deteriorated, leaving detached ears and jaws to be invaded. A few adult muscids were also observed and collected. Adult *Prochyliza xanthostoma* Walker (F. Piophilidae) and *Stearibia nigriceps* (Meigen) (F. Piophilidae) were collected in both sunny and shaded areas (Figure 12). *Stearibia nigriceps* was the most abundant species and adults were collected from pig carcasses from Day 6 to the end of the sampling period. Adults of *Prochyliza xanthostoma* were also observed and collected on Day 6 and were present on sun-exposed pigs until Day 10 and on shaded pig carcasses until Day 17 (Figure 12).

Adult *N. surinamensis* were collected from carcasses in the sunny area on Day 6 and were present for around 18 days. The larvae of *N. surinamensis* were observed on Day 6 and were recorded until Day 24 on pig carcasses in both sunny and shaded areas. Basically, both *N. surinamensis* adults and larvae were most abundant and arrived during the peak maggot period (Figure 13). Adults of *Oiceoptoma*

noveboracensis (Forster) (F. Silphidae) were observed and collected in the shade by Day 6 and were not observed in the sun until Day 342. Larvae of this species were infrequent and occurred on the shaded carrion on Day 8 (Figure 13). Adult clerids were collected from carcasses in both sun and shade (Figure 15). *Necrodes rufipes* (DeGeer) (F. Cleridae) and *Necrodes violacea* (Linnaeus) (F. Cleridae) were collected in both sunny and shaded areas (Figure 15). Adults of *Necrodes rufipes* arrived much earlier than did those of *N. violacea*. Adults of *N. rufipes* occurred on carcasses in the sun on Day 6 and on carcasses in the shade on Day 8, whereas *N. violacea* occurred in the sun on Day 24 and in the shade on Day 17. Both species were most prevalent in the sun than in the shade and *N. violacea* were abundant immediately following the winter period, until the last sample date (Figure 15). It should also be noted that this is the first report of *N. violacea* from Manitoba.

Nitidula ziczac Say (F. Nitidulidae) was observed sooner in the shade (Day 6) than in the sun (Day 24). This species was numerous and continually present throughout the entire sampling period (Figure 16).

WEEK II:

Abundance of adult *P. regina* dissipated by Day 7 in both sunny and shaded areas (Figure 11). This is reflected by the first break in the bar on Day 7 that occurred during the beginning of the peak maggot period. The mean internal carcass temperature reached its maximum in the sun on Day 8 (36.7C) with an air temperature of 27.9C (Figure 22). Maggot activity in the head area of the sun-exposed carcasses had decreased considerably by this time and there were still thousands of larvae

moving and feeding in the torso. By Day 8, the carcasses in the shaded area were in the decay stage of decomposition and maggot activity was reaching its peak (Figure 18 and 20C, D). On Day 9, a maximum mean internal carcass temperature in the shade was recorded at 37.6C. The mean ambient air temperature on this day was recorded in the shade at 24.3C (Figure 23).

In pitfall collections, the majority of calliphorid larvae entered the wandering stage within the second week of pig placement. Mean numbers of maggots collected in each pitfall trap were variable. The numbers of calliphorid maggots in pitfall collections on Day 9 associated with sun-exposed pig carrion ranged from 33 to 3,499 maggots per trap. The mean number of maggots collected from pitfall traps surrounding pig carcass B was 950 (± 850 SE; n=4) and a mean number of 433 (± 258 SE; n=4) maggots was collected from pig carcass D (Table 2). Maggots collected from pitfall traps in association with shaded carrion ranged from 55 to 3,903 maggots per trap. The mean number of maggots collected from pig carcass A was 1,001 (± 470 SE; n=4) and the mean number associated with pig carcass C was 2,009 (± 734 SE; n=4) (Table 2).

From collections from the four pitfall traps situated around each carcass, the maggots did not disperse uniformly away from the carcass. Estimated numbers of maggots collected from pitfall traps were greatest for all four carcasses in an eastward direction in both sunny and shaded areas. In addition, maggots were found in one of the distal pitfall traps in the shade, so larvae had travelled at least 15m away from the carcass.

Many magpies, crows and ravens were seen feeding on the maggots through the cage grids and from the mounds of maggots that had wandered away from the carcasses. Some also scavenged bits of pig carrion through the cage grids. Maggots that had wandered away from some carcasses had left noticeable trails of matted down grass behind them. There was a huge mass of maggots found approximately 30cm in a southeast direction away from one cage. On Day 10, close to one of the shaded pig cages, ten maggots had climbed 1m above ground and settled into the hollow of a broken tree branch.

After this time, there was a drastic decrease in internal carcass temperatures for both sun and shade-exposed pig carcasses. By Day 10, the mean internal carcass temperature of sun-exposed carcasses was 30.5C and the ambient air temperature was 28.0C (Figure 22). Similarly, in the shade, the mean internal carcass temperature was recorded at 27.9C with a corresponding air temperature of 25.1C (Figure 23). As time progressed, the mean internal carcass temperatures began to fluctuate nearer to the mean ambient air temperature in both sunny and shaded areas and ambient and internal temperatures were similar for the remainder of the sample period (Figures 22 and 23). Overall, the mean ambient and internal carcass temperatures were higher in the sun than in the shade.

On Day 10, the mean pig carcass mass in both sun and shade were the same (22.5kg) and at which point the mass of the shade-exposed carrion became and continued to be less than in the sun (Figure 21). It was noted that the carcasses in the sunny area retained more water and took longer to dry due to precipitation combined

with poor drainage. Overall, the carcasses in both sun and shade seemed to lose mass at approximately the same rate.

Adult *P. regina* reappeared on Day 13 in the sun and on Day 10 in the shade (Figure 11). Completion of pupal development was signified by the start of the emergence of adults from the carcasses. This development of the second-generation adults from the pig carcasses in the sun took at least 15 days. The emergence of second generation *P. regina* adults was evident in the shade for a significantly longer period of time (Figure 11). Completion of development for these flies took a minimum of 32 days. By Day 13, activity of calliphorid larvae decreased substantially and there was a considerable decrease in the numbers found on the carcasses. Many other insects, such as adult piophilids, sphaerocerids, sepsids, muscids, clerids, histerids, scarabs and various beetle larvae were actively moving around in the pasty areas of the carcasses. Much of the skin was dried on the head and very little insect activity was apparent there (Figure 20).

WEEKS III AND IV:

Calliphorid larvae were still in the wandering stage of development at the beginning of the third week, as evidenced by their presence in pitfall traps. Collections from pitfalls surrounding sun-exposed carrion ranged from 1 to 3,354 maggots per trap. Mean numbers of maggots associated with pig carcass B were 1,471 (± 848 SE; n=4) and the mean number of maggots collected from pitfalls around pig carcass D was 94 (± 53 SE; n=4) (Table 2). Pitfall trap collections in the shaded area ranged from 3,360 to

14,159 maggots per trap. The mean number of maggots associated with pig carcass A was 7,875 (± 2177 SE; n=4) and the mean number of maggots in pitfall traps around pig carcass C was 6,861 (± 2,486 SE; n=4) (Table 2).

By Day 10, the carcasses in the sunny area had reached the beginning of the advanced decay stage; the advanced decay stage began in the shaded area after Day 13 (Figure 18 and 20E). This stage was approximated visually and was based on the marked decrease in numbers of maggots associated with each pig carcass.

Overall, by Day 15, maggot activity in the carrion had decreased dramatically. There were few third instar calliphorids left and there were puparia within the clothing layers. A few adult Sarcophagidae were observed flying around the carcasses. Adult *Calliphora vicina* Robineau-Desvoidy (F. Calliphoridae) and *Lucilia illustris* (Meigen) (F. Calliphoridae) were also collected from pig carcasses in the sun (Figure 11). These two species were found later in the arrival sequence. *Lucilia illustris* was first observed on Day 20 and then occurred sporadically on Days 24, 51 and again on Day 349. Adults of *L. illustris* were collected in the shade on Days 22, 48 and 382. Adult *Calliphora vicina* were collected from pig carcasses in the sun on Day 24 and were not observed or collected after this day (Figure 11).

Many adult and larval silphids were observed during this time, mostly *N. surinamensis*. Many of the clerids and nitidulids inhabited the drier regions of the carcasses. Many different species of adult staphylinids were present. Adults of *Ontholestes cingulatus* were sporadic in terms of its arrival and duration of stay (Figure 14). These beetles were observed and collected on Days 2, 51, 55, 356 and 382 in the sun. This species was not observed in the shade until Day 15 and was collected again

on Day 24 (Figure 14).

Pitfall collections of maggots during Week 4 had decreased significantly. There were no maggots found in pitfall traps surrounding pig carcass B and only one calliphorid larva was found associated with pig carcass D. Similarly, there were only three maggots associated with pig carcass A and none were collected from pitfall traps near pig carcass C (Table 2).

By Day 27, all calliphorid larvae and adults were gone. The third instar larvae of the Piophilidae were observed in masses in the pasty regions of the carcasses. These were collected from the pig carcasses on Day 27 in both the sunny and shade areas (Figure 12).

WEEK V TO FIRST FROST:

No significant changes occurred in relation to the rate of carrion decay and insect diversity, abundance and/or activity during this period of time. Observations and samples were, therefore, taken on a less frequent basis.

POST-WINTER PERIOD:

Numerous adult *Stearibia nigriceps* were observed and collected from pig carcasses in both sunny and shaded areas immediately following the winter period (Figure 12). The assumption that this species over-wintered as late instar larvae and/or pupae and completed its adult development at first thaw was extrapolated from the collection of several teneral adult piophilids immediately following thaw (Figure 12). Adults of this species were observed on Day 321 in the sun and shade and stayed on the sun-exposed carrion until Day 375 and on shaded carrion until Day 349 (Figure 12).

There were no third instar piophilid larvae in the shaded area following the winter period and after Day 329, there were no piophilid larvae seen on the carcasses in the sunny area (Figure 12). Only a few adult *L. illustris* were collected following the winter period, specifically on Days 349 and 382 (Figure 11).

Nitidula ziczac and *Glischrochilus quadrisignatus* (Say) (F. Nitidulidae) were the predominant nitidulid species collected from pig carrion throughout the summer trial at Glenlea Research Station (Figure 16). Adult *N. ziczac* first appeared on carrion in the shaded area in the first week and in the fourth week in the sunny area. *Glischrochilus quadrisignatus* was most prevalent on the carrion in the shade and was collected after the winter period in both sun and shade (Figure 16). This species was more common on shaded pig carrion. Adults of *Glischrochilus quadrisignatus* were collected consistently from Days 321 to 382 in the shade, for a duration of 62 days and were observed sporadically on pig carrion exposed to sun on Days 329 and 382 (Figure 16).

Members of the family Dermestidae were not strongly represented in this trial. Adult *Dermestes fasciatus* LeConte (F. Dermestidae) and *Dermestes lardarius* Linnaeus (F. Dermestidae) were the two main species collected from pig carrion (Figure 16). Adult *Dermestes lardarius* occurred sporadically on pig carrion in the sunny area on Days 27 and 329 and in shade on Days 37 and 76 (Figure 16). Adult *Dermestes fasciatus* was only observed and collected in the sunny area on Days 321 and 349 (Figure 16) and one adult *Dermestes signatus* LeConte (F. Dermestidae) was found on pig carrion in the shaded area on Day 329. Many scarabs, staphylinids, carabids and clerids were observed and collected from all pig carcasses.

The Trogidae were weakly represented in the summer trial at Glenlea Research

Station (Figure 17). One adult *Trox unistriatus* Beauvois (F. Trogidae) occurred on a pig carcass in the sun on Day 6 but this species was prevalent after the winter period from Days 335 to 349. This species occurred on shaded carrion from Days 342 to 349 and again occurred singly on Day 382 (Figure 17). No species of Geotrupidae were found at Glenlea Research Station (Figure 17). These beetles are typically found in areas with sandier soil types. It was therefore suspected that since this region is predominantly clay soil, these beetles are not typical of this area.

All carcasses were still mouldy, wet and pasty in places. These areas and the drier regions hosted many species of insects. Mice and voles had also inhabited the pig carrion and had used the inside of one carcass to rear its young. By Day 355, most regions of the carcasses in the shaded area were very dry. However, sun-exposed and shaded carcasses seemed to re-hydrate with high humidity and rainfall and as a result, it was difficult to establish the beginning of the dry remains stage. Fly larvae were only found on the moist parts on sun-exposed carrion. The carcasses in the shaded area continued to house many beetle species such as the nitidulids, clerids, carabids, histerids and staphylinids. Mite aggregations were also observed on the drier carcasses. Sweep samples and hand collections were largely discontinued after this time; however, observations of insect occurrence were maintained. By Day 398, all fly activity had ceased and all that remained on the carcasses were adult *Necrodes* spp., *N. ziczac* and nitidulid larvae. By this time, most of the moist regions of the sun-exposed pig carcasses had become dry. Since there were no longer any fly larvae on the carrion, it was determined that the dry remains stage had been reached (Figure 20F). On the last sample day, 01 September, 1999 (Day 426), all carcasses still hosted

numerous adult and larval nitidulids, adult and larval dermestids and adult clerids, carabids and histerids (Appendix 1).

SANDILANDS PROVINCIAL FOREST - FALL TRIAL

The fall trial at Sandilands Provincial Forest began on 29 August, 1998 (Day 0). Eight pigs were killed, clothed, stabbed and placed in cages. HOBO® temperature data loggers were situated in both sunny and shaded areas to measure internal carcass and ambient air temperatures. On specific sample dates each carcass was photographed and observed for insect activity. Observations and insect sampling ceased at first frost on 01 October, 1998. Sampling resumed after the winter period at first thaw. This time period will be collectively referred to as the post-winter period (13 May, 1999 to 31 August, 1999).

The data loggers malfunctioned during this trial; therefore none of the internal carcass temperatures were recorded from the pig carcasses in the sunny area. For this reason only mean ambient air temperatures are illustrated in Figure 34.

At the same time as the above ground carrion study, a strenuous effort was made to study the insect succession and decomposition of buried carrion. Six additional 70kg pig carcasses were clothed, stabbed, placed in graves and buried with internal temperature loggers (Figure 32A). Unfortunately, by Day 16 all buried pig carcasses had been dug up and mostly eaten by what we suspected to be wolves. An attempt was made to re-bury parts of the carcasses, but scavengers had returned and devoured the rest of the pig carrion. It should be noted that since the summer trial at Glenlea Research Station was still on going and increased intensity of insect sampling was required for the fall trial, it was decided that the collection of weight data would not be collected during this trial.

WEEK I:

On Day 0, internal carcass temperatures for three shade-exposed pig carcasses were recorded as 30.2C, 28.2C and 27.7C, respectively. This was 8 - 11C higher than the mean ambient air temperature (Figure 35). The ambient air temperature in the sun was 23.3C, which was 3.6C higher than in the shaded area (Figure 34).

On Day 0, adult calliphorids were attracted to and actively laying eggs in and around the wounds on pig carcasses in sunny and shaded areas (Figure 32B, C). *Phormia regina* was the most abundant blow fly species. These adults were present on carrion in the sunny area until Day 10 and in the shaded area until Day 26 (Figure 24). Adults of *Calliphora vomitoria* (Linnaeus) (F. Calliphoridae) and *Lucilia illustris* were also observed and collected from pig carrion in sun and shade on Day 0 (Figure 24). Adults of *Calliphora vomitoria* were present until Day 5 on sun-exposed carrion and until Day 8 in shaded carrion and were not observed again until Day 290. Adult *L. illustris* were collected from the carcasses for the first 9-10 days in both sun and shade (Figure 24).

By Day 1, all pig carcasses were sporting hundreds of thousands of calliphorid eggs in the mouth, nostrils, in and behind ears, under the eyelids, and within blood soaked areas and folds of the clothes. First instar calliphorid larvae were observed in both sunny and shaded areas. Several vespids were observed flying in and around the carcasses and were seen feeding in blood pools and on adult calliphorids. Tiny staphylinids and ants were seen carrying bundles of calliphorid eggs away from the carcasses.

On Day 2, there were thousands of first instar calliphorids on all carcasses. Hundreds of adults were still actively ovipositing, and on one carcass, resorted to laying

hundreds of thousands of eggs in the anal opening. By this time, the head regions of most carcasses began to swell and turn green.

Bloat began on Day 3 in both sunny and shaded areas. There was no difference in the rate of decay in sunny and shaded areas for the first two stages of carrion decomposition (Figure 31 and 33A and B). The mean ambient air temperature in the shade was 12.7C and 15.3C in the sun and the internal carcass temperatures for shaded pig carcasses A, Ec and Gc were 15.4C, 16.7C and 17.4C, respectively (Figures 34 and 35). Several *Nicrophorus* spp. were observed and collected as adults in and around egg masses on the shaded carrion. Adult *Geotrupes semiopacus* Jekel (F. Geotrupidae) were observed and collected and were present until Day 22 (Figure 30). Those of *Nicrophorus* and *Geotrupes* were more evident on pig carrion in the shade (Appendix 1).

By Day 4, eggs, first and second instar larvae were the dominant insects on the pig carcasses. *Vespula* spp. and *Dolicovespula* sp. (F. Vespidae) were capturing and feeding on adult calliphorids. One hornet was seen stinging an adult calliphorid before it chewed its head off and then flew to a nearby tree where it continued to feed on it. A single specimen of *Dermestes lardarius* was observed and collected on Day 4 from a sun-exposed pig carcass (Figure 29).

On Day 5, third instar calliphorid larvae became evident; however, firsts and seconds were dominant. Adult *S. nigriceps* arrived at carcasses on Day 5 and were consistently present until Day 26 in the sunny area. This species was first observed on Day 10 in the shaded area (Figure 25). Three adult *G. semiopacus* were observed

constructing burrows, approximately 1cm in diameter, in the sand along the edge of a cage in the shade.

On Day 6, the mean ambient air temperature in the sunny area was 24.3C and 20.2C in the shaded area (Figures 34 and 35). The internal carcass temperatures of pigs A, Ec and Gc were recorded as 18.9C, 17.6C and 12.8C respectively (Figure 35). Due to blow fly larvae feeding, the skin on the carcasses was beginning to recede in the head and leg areas. During the first week, seven third instar sarcophagid larvae were collected from pitfall traps associated with pig carcass B.

WEEK II:

The decay stage in both sunny and shaded areas was evident by Day 9 (Figure 33C and D). On this day, the mean internal carcass temperature of pig carcass A reached its maximum at 32.8C (Figure 35). The majority of maggot activity was observed in the same area as the temperature probe, in the chest area underneath the shirt, where third instar maggots dominated (Figure 33D). Internal carcass temperatures of pigs Ec and Gc increased to 20.5C and 19.1C, respectively. The mean ambient air temperature on this day was 11.0C and the mean ambient air temperature in the sun was 13.4C (Figures 34 and 35).

On Day 10, eggs, first, second, and third instar calliphorid larvae were still developing on pig carrion in both sunny and shaded areas. In some cases, maggots were spilling out from the cages onto the ground and third instar larvae began to accumulate in masses adjacent to the cages in both sun and shade. Adults of *Stearibia nigriceps* were observed and collected from the shaded carrion on Days 10 to 17 and

were not seen again until the post-winter period (Figure 25). *Prochyliza xanthostoma* were not very abundant; however, a few adults were collected in both sun and shade on Day 10 (Figure 25).

On Day 11, the internal carcass temperature of pig carcass Gc reached its maximum of 40.1C. The ambient air temperature in the shade on this day was 19.1C. On this date, the internal carcass temperature of pig carcass A decreased to 29.7C and the internal carcass temperature of pig carcass Ec was 27.2C (Figure 35).

On Day 12, the internal carcass temperature of pig carcass Ec reached its maximum temperature of 31.2C. There was a huge mass of maggot activity below the belly region of the carcass. The ambient air temperature in the shade on this day was 22.7C (Figure 35). By Day 12, a huge number of maggots had begun to wander away from the sun-exposed carcasses. This indicated the beginning of the advanced decay stage for sun-exposed carrion. Maggot activity on the shaded carrion was still excessive; however, many of the pitfall traps were overflowing with maggots. As a whole, the beginning of the advanced decay stage occurred two days later for the shaded pig carcasses (Figures 31 and 33C and D).

Within the second week, pitfall trap catches ranged from 1,517 to 7,649 calliphorid maggots wandering from sun-exposed pig carrion. A mean number of 2,575 (± 418 SE; n=4) maggots were collected in pitfalls associated with pig carcass B and 4,965 (± 907 SE; n=4) were collected in pitfalls around pig carcass D (Table 2). Estimated numbers of maggots collected in eight pitfall traps associated with the shaded carrion ranged from 1,546 to 9,608. The mean number of maggots collected from pitfall traps surrounding pig carcass A was 4,612 (± 1792 SE; n=4) and a mean of

4,168 (± 957 SE; n=4) maggots was recorded from pitfalls around pig carcass C (Table 2). It should be noted that not all maggots that wandered into pitfall traps were killed. Many maggots were still alive when pitfall traps were collected. The preservative became so saturated with maggots that these traps no longer effectively killed the larvae. There was no indication of directional bias for maggots in the wandering stage during this trial.

WEEKS III, IV AND V:

On Day 14, there was still maggot activity on the carcasses; however, the largest portion of the maggots had moved away from the shaded carrion (Figure 33E). Pre-pupae and pupae were observed in the layers of clothing and were found in the soil near the cages. Many adult sarcophagids, muscids, sepsids and piophilids were observed on the carrion and vespids continued to feed on adult flies.

After Day 14, the internal carcass temperature of pig A began to follow that of the ambient air temperature and this continued until the end of the sample period (Figure 35). The mean ambient air temperature in sun and shade was approximately 15.2C (Figures 34 and 35). Pig carcasses Ec and Gc began to follow the fluctuations in air temperature; however, the internal temperatures of these carcass means were 4-9C higher than the air temperature until Day 33, the end of the sampling period (Figure 35). It should be noted that there were still small masses of third instar maggots associated with pig carcasses Ec and Gc on Day 17. The second generation of *P. regina* was denoted by the presence of teneral adults. Newly emerged *P. regina* were collected from shaded and sun-exposed carrion on Day 17 until the last sample day before the

winter period (Figure 24). There was an obvious seven-day lag in the presence of adult *P. regina* in the sunny area. There was no break between the presence of the first and second adult generation *P. regina* on the shaded carrion (Figure 24). Beetle activity began to increase significantly during this period of time. Larval staphylinids and *N. surinamensis* were observed and collected on sun-exposed pig carrion on Days 17 to 26 and a few were collected on Day 26 on the shaded carrion (Figure 26). Adults of *N. surinamensis and O. noveboracensis* seemed to arrive much later in the decay process during the fall trial compared to the summer trial.

By Day 21, the mean ambient air temperature was 11.5C in both sunny and shaded areas (Figures 34 and 35). After heavy rainfall, all carcasses were saturated with water. Insect activity on this collection day had decreased dramatically. Calliphorid larvae and adult *P. regina* were observed on the carcasses and were moving very slowly. Most insects had retreated within the clothes, underneath the carcass and within skeletonized portions of the head. A few adult *N. surinamensis* were observed on shaded carrion from Days 22 to 33 (Figure 26). Adult *C. maxillosus* were observed and collected from pig carrion on Days 22 to 33 in the shaded area but were not observed in the sunny area until the post-winter period (Figure 27).

The numbers of maggots in pitfall traps decreased considerably during Week 4. There were only three calliphorid maggots collected in pitfall traps from pig carcass B and only one maggot was collected from pig carcass D (Table 2). Pitfall trap catches from shaded carrion ranged from 5 to 65 maggots per pitfall trap. The mean number of maggots associated with pig carcass A was 18 (± 5 SE; n=4) and a mean of 50 (± 10 SE; n=4) maggots were collected in pitfall traps around pig carcass C (Table 2).

On Day 26, the mean ambient air temperature in the sunny and shaded areas was 9.6C. Third instar larvae were still present on both sunny-exposed and shaded carrion and numerous adult calliphorids were emerging from puparia. Adult piophilids were also abundant and seen mating on the carcasses. Second instar piophilid larvae were observed on pig carrion in both sunny and shaded areas (Figure 25). It should be noted that these larvae were most abundant during the post-winter period. From Day 27 to 33, no noticeable changes took place in relation to the rate of carrion decomposition, insect activity and abundance, and the types of insects present.

During Week 5, another mass of maggots had wandered away from pig carcass C. A mean number of 877 (± 366 SE; n=4) maggots were collected in pitfall traps (Table 2). By this time, pitfall collections in the sunny area had decreased to two maggots associated with pig carcasses B and D and the mean number of maggots found in pitfalls associated with pig carcass A was 37 (± 16 SE; n=4) (Table 2).

On Day 33, the mean ambient air temperature had decreased to 3.7C (Figures 34 and 35). This was the last sample day scheduled for the season since the first heavy frost had occurred on the previous night.

POST-WINTER PERIOD:

Observations and insect sampling resumed on Day 258 (13 May, 1999). During this time, the carcasses consisted mostly of bones with moist, pasty areas that still harboured fly larvae. Piophilid larvae and adult *Stearibia nigriceps* were most abundant after the winter period (Figure 25). Both adults and larvae were collected from sun-exposed pig carrion on Day 258 and were present in all collections up until Day 311.

These larvae were collected from Days 258 to 318 in the shade. Teneral adult piophilids were first observed in the shaded area on Day 269. These adults were present until Day 304 (Figure 25). Adults of *Prochyliza xanthostoma* occurred sporadically. This species was observed and collected in small numbers on Day 258 from sun-exposed and shaded carrion and again on sun-exposed carrion on Day 269 (Figure 25). Third instar calliphorid larvae were still found living in the shaded carrion from Days 258 to 262. Adult *C. maxillosus* were present from Days 258 to 276 in the shaded area and a single specimen was collected on Day 269 on sun-exposed carrion (Figure 27).

Few adults and no larval *O. noveboracensis* were collected throughout this trial. Adults of this species were collected from sun-exposed carrion from Days 258 to 276 and only one specimen was collected in the shade on Day 258 (Figure 26). *Necrodes violacea* was the predominant clerid collected as an adult during the fall trial (Figure 28). This species was collected from pig carrion during the post-winter period from Days 258 to 360 in sun and from Days 269 to 360 in the shaded area (Figure 28). A few adult *N. rufipes* were collected from pig carrion in the sunny area. This species was collected on Day 26 and then was observed again from Days 258 to 262 (Figure 28). *Nitidula ziczac* was the only nitidulid species to arrive as an adult on carrion during the fall trial (Figure 29). There was no difference in timing of arrival and duration of stay in sunny versus shaded areas. Adults of *N. ziczac* arrived on Day 258 and were collected from the pig carcasses until Day 360 (Figure 29).

A few specimens of adult *L. illustris* were collected in the sunny area from pigs after the winter period. This species was periodically observed and collected from Days

262 to 276 (Figure 24). *Necrodes surinamensis* larvae were present to the same extent in both sunny and shaded areas immediately following the winter period and were collected from Days 269 to 311 (Figure 26). Adult *P. regina* occurred sporadically on Days 283 to 290 and then were not seen again until Day 325 (Figure 24). Adult *O. cingulatus* were collected from Days 283 to 304 and seemed most prevalent on carrion in the shade. Only one specimen was collected on Day 290 from a carcass in the sun (Figure 27). One adult *C. vomitoria* was collected from a carcass in the shade on Day 290 (Figure 24).

Very few specimens of Dermestidae were observed during this trial. Besides the single specimen found on Day 4, *D. lardarius* was collected from pig carcasses in the sun on Days 297 and 360 (Figure 29). Similarly, *Dermestes ater* DeGeer (F. Dermestidae) was observed intermittently on carrion in the sun from Days 258 to 269, Day 297 and Day 325 and in the shade on Day 258 only (Figure 29). Adults of *Trox unistriatus* arrived at the pig carcasses earlier in the shade (Day 283) than in the sun (Day 304) during the fall trial (Figure 30). *Geotrupes* occurred sporadically, as early as Day 3 and as late as Day 283 (Figure 30).

The dry remains stage was difficult to distinguish from the advanced decay stage since different regions of the pig carcasses dried out sooner than others. As a result, insects considered to be attracted to the dry remains stage were often present in concurrence with fly larvae feeding and developing in moist areas of the same carcass. Distinction of the dry remains stage was therefore determined by the absence of all fly larvae in the carrion. Based on this, it appeared the sun-exposed carrion reached the dry remains stage by Day 311. The shaded carrion reached this stage by Day 353

(Figure 33F). At this point, the dried carcasses were used as dwellings for small squirrels, spiders and toads. On the last sample date, 31 August, 1999 (Day 367), all carcasses harboured adult dermestids, nitidulids, clerids, trogids, staphylinids, histerids and carabids (Appendix 1).

ELM CREEK – SPRING TRIAL

The spring trial at Elm Creek began on 29 May, 1999 (Day 0). Eight pigs were killed, clothed, stabbed and placed in cages. HOBO® temperature data loggers were situated in both sunny and shaded areas to measure internal carcass and ambient air temperatures. On specific sample dates, one sun-exposed and one shaded carcass were weighed. All carcasses were photographed and observed for insect activity. Observations and insect sampling ceased at first frost on 02 November, 1999. Sampling resumed and continued for a three-week period after the winter at first thaw. This time period will be collectively referred to as the post-winter period (01 to 15 May, 2000).

Due to mechanical problems with the data loggers during the spring trial at Elm Creek, only mean daily ambient air temperatures were recorded in the sunny and shaded areas (Figure 47).

WEEK I:

Day 0 was the first day of the fresh stage of decomposition (Figures 43 and 45A). Both carcasses weighed 68.0kg (Figure 46). The mean ambient air temperature in the sunny area was 23.8C and in the shade was 21.5C (Figure 47). Adult *Phormia regina* were immediately attracted to the carcasses and observed on pig carrion in both sun and shade (Figure 36). This was the key calliphorid species present and adults were collected from sun-exposed carrion from Days 0 to 11 and on shaded carrion from Days 0 to 9 (Figure 36).

By Day 1, the mean ambient air temperature had decreased to approximately 11C (Figure 47). Evidence of calliphorid oviposition was apparent in the wound areas,

mouths, and ears and under the eyelids of both shaded and sun-exposed carrion (Figure 44A). Many of the adult calliphorids were slow moving and seeking refuge within the clothing layers of the carcasses, where they were seen laying eggs in these areas. Adults of *Lucilia illustris*, *Cynomya cadaverina* (Robinaeau-Desvoidy) (F. Calliphoridae) and *Protophormia terraenovae* (Robineau-Desvoidy) (F. Calliphoridae) were present to a lesser extent during the first 11 days (Figure 36). *Stearibia nigriceps* was the most abundant piophilid species attracted to pig carrion in both sunny and shaded areas. These adults arrived at the pig carcasses on Day 3 in the sun and on Day 1 in the shade (Figure 37). Sphaerocerids, ticks, ants and *O. cingulatus* were also observed in association with the carrion (Figure 39). The ants and staphylinids were removing and feeding on calliphorid eggs.

By Day 2, first instar calliphorid larvae were established on all of the sun-exposed and shaded pig carcasses. On Day 3, the mean ambient air temperature was 10.5C in the shade and 11.9C in the sun (Figure 47). Some of the carcasses began to bloat and turn green in the head area. Adults of *Ontholestes cingulatus* were frequently observed on both shaded and sun-exposed pig carrion throughout the first 157days (Figure 39). *Geotrupes semiopacus* were also well represented. This species was observed on shaded carrion and collected from pig carcasses from Days 3 to 104. This species only occurred sporadically on sun-exposed carrion and was observed on Days 11 and 111 (Figure 42). Second instar calliphorid larvae were observed on Day 4 and by this time all of the carcasses were showing minor signs of bloat and discolouration.

By Day 6, the mean ambient air temperature increased to 21.3C in the shaded area and 27.3C in the sunny area (Figure 47). Both carcasses experienced a small decrease in

mass; each weighed 65.8kg (Figure 46). However, the sun-exposed carcasses were more bloated than the shaded carcasses (Figure 45B).

WEEK II:

On Day 7, mean ambient air temperatures were 22.9C and 19.5C in sun and shade, respectively (Figure 47). All sun-exposed carcasses were in the bloat stage of decay (Figure 43 and 45B). Adult *O. noveboracensis* were abundant on both sun-exposed and shaded carrion (Figure38). Adults of *Creophilus maxillosus* arrived around Day 8 and were persistently associated with the pig carcasses for the majority of the sample period in both sunny and shaded areas (Figure 39).

On Day 9, the mean ambient air temperature in the shade was 19.6 C and 18.5 C in the sun. First and second instar maggot activity was still high and third instar calliphorids were apparent on both sun-exposed and shaded carrion. By Day 9, all of the shaded carcasses were in the bloat stage of decomposition (Figure 43). The sun-exposed carcasses continued to decompose as larval feeding in the head area caused the tissue to split apart. One of these carcasses remained bloated in the lower portion of the body while its skin in the upper region had completely receded exposing distended internal organs (Figure 44C).

Adult *Necrodes surinamensis* arrived on the pig carcasses between Days 9 and 11. By Day 13, *N. surinamensis* larvae were evident on the carcasses in the sunny area. *Nitidula ziczac* were observed in large numbers on carrion from Days 9 to 157 (Figure 41). Adults of *Trox unistriatus* were also collected from pig carrion in the shade as early as Day 9 and were present until Day 86. This species was observed on sun-

exposed carrion from Days 12 to 74 (Figure 42). Many of the trogids collected were infested with red mites. Some of the more heavily infested individuals were found dead in and around the carcasses. Adults of *Dermestes ater* occurred sporadically on shade carrion from Days 10 to 89 (Figure 41).

On Day 12, the mean ambient air temperature in the sun was 21.3C and 19.6C in the shaded area (Figure 47). By this time, all of the sun-exposed carcasses were deflated and at the decay stage of decomposition (Figure 45C and D). The head area of these carcasses was completely devoured and huge masses of third instar larvae were actively feeding in the upper and lower areas of the body. The reddish gut contents of these actively feeding third instars can be seen in Figure 44B.

The mass of the sun-exposed carcass rapidly decreased to 34.0kg by Day 13 and the shaded carcass weighed 63.0kg (Figure 46). By this time the shaded carcasses were in the decay stage of decomposition. Many adult piophilids were observed and collected and some were seen mating. Many larval and adult beetles were active within the carrion. There were still blow fly eggs, first and second instar larvae developing on all of the carcasses. Calliphorid pre-pupae and pupae were found on carrion and on the ground in the shaded area.

Within the second week, the mean pitfall trap collection was 3 (± 2 SE; n=4) calliphorid maggots per trap associated with pig carcass B and 35 (± 14 SE; n=4) maggots per trap for carcass D (Table 2). Similarly, a mean of 7 (± 3 SE; n=4) maggots per trap were collected from pitfalls around pig carcass A and 24 (± 9 SE; n=4) maggots per trap in relation to pig carcass C (Table 2).

WEEK III:

Adult calliphorids, sarcophagids, muscids, piophilids and sepsids were observed on all of the carcasses at this point. Adult clerids, nitidulids, histerids, scarabs, silphids and staphylinids were also observed on carrion in both sunny and shaded areas. *Glischrochilus quadrisignatus* occurred sporadically on Days 17 and 24 on sun-exposed carrion (Figure 41). Adult *N. rufipes* was present on sun-exposed carrion from Days 18 to 104 and sporadically on shaded carrion from Days 17 to 20, Day 58 and Days 97 to 157 (Figure 40). Adults of *Necrodes violacea* were not observed until Day 48 in the sun and on Day 97 in the shade. However, both species were present in equal abundance during the post-winter period (Figure 40).

On Day 16, the mean ambient air temperature decreased to 10.8C in the shaded area and 14.0C in the sunny area (Figure 47). By Day 17, many of the third instar maggots associated with the sun-exposed carrion reached the wandering stage of development. This was the first indication of the advanced decay stage (Figures 43 and 45E). On Day 18, there were still huge maggot masses associated with the shaded carrion; however, there was evidence that some of the maggots had begun to wander away from the carcass in search of pupation sites. By Day 20, the sun-exposed pig carcass had decreased in mass to 16.8kg and the shaded carrion weighed 49.9kg (Figure 46).

WEEK IV TO FIRST FROST:

By Day 23, the shaded carrion had reached the beginning of the advanced decay stage (Figure 43). On Day 24, the mean ambient air temperature in the shaded area was 24.2C and 27.8C in the sunny area (Figure 47). Evidence of the emergence of

second-generation adult *P. regina* was seen on Day 24 in both sun and shade. By Day 29, the sun-exposed carrion levelled off at 14.0kg and the shaded carcass decreased to 25.9kg (Figure 46). By Day 3, there was a significant decrease in numbers of maggots in the pitfall traps located in the shaded area (Table 2).

On Day 33, there were still pupae and third instar calliphorid maggots on all of the carcasses. Nitidulid larvae and adult silphids, staphylinids, piophilids, sepsids and teneral calliphorids were also present. Second instar piophilid larvae were observed on pig carrion in the sun on Day 39 and in the shade on Day 41 (Figure 37). By Day 44, piophilid larvae were the most abundant fly species present on the carcasses. There were few calliphorid larvae remaining.

By Day 48, all carcasses contained a plethora of insect species. Piophilids were mating; sepsids were mating. Adult sarcophagids, muscids and calliphorids, adult and larval nitidulids, clerids, histerids, carabids, scarabs, geotrupids, silphids, staphylinids and mites were also present. All of these species were present until the end of the sample season. Overall, the carcasses were dry in the head region and were moist and pasty in the body region. Few changes occurred after this time in terms of the state of decay and insect diversity and activity until Day 86. At this point, the shaded carrion had begun to dry out and as a result, fewer fly larvae were present. The sun-exposed carrion was much moister and still accommodated many piophilid and muscid larvae.

After Day 97, observations were reduced to a weekly basis until the end of the sample season. No significant changes occurred relative to insect diversity during this period.

POST-WINTER PERIOD:

Sampling resumed after the winter period on Day 333 (01 May, 2000). The top portions of the carcasses were very dry and bleached in appearance; however, the carcasses were very moist near the ground surface. Adult clerids, histerids, silphids, staphylinids, dermestids, carabids, red ants, mites and spiders were observed and collected from pig carrion for the remainder of the study period in sunny and shaded areas. Many of the ants and staphylinids were seen carrying piophilid larvae away from the carcasses. Overall, adults of *N. ziczac* were the most abundant beetle present on the carcasses and were consistently present for the entire post-winter period (Figure 41). Adults of *Glischrochilus quadrisignatus* were collected from sun-exposed carrion and were only observed once on Day 340 in shaded carrion (Figure 41). The dermestids were present in small numbers. Adults of *Dermestes lardarius* were collected from sun-exposed pig carrion from Days 333 to 347 and only one adult specimen of *D. ater* was observed in the shade (Figure 41).

Adult muscids and sphaerocerids were also observed flying around and crawling within the carcasses. Third instar piophilid larvae and pupae were also collected (Figure 44D). Pupae and newly emerged adults of *S. nigriceps* were observed and collected from sun-exposed carrion until the last sample date which was 15 May, 2000 (Figure 37). Since by Day 347 most of the fly larvae were gone, it was considered the beginning of the dry remains stage (Figure 45F). Most of the piophilids had developed into pupae and teneral adults were observed emerging from the shaded carrion (Figure 37). Adult *P. regina*, *L. illustris* and *C. vomitoria* were observed flying around one of the sun-exposed carcasses.

CHAPTER 5
DISCUSSION

The main objective for this study was to collect and identify the insect species for part of their life cycle associated with pig carrion comparatively in sunny and shaded areas in rural Manitoba. Furthermore, this study was to contribute information related to forensic entomology in Manitoba, for the development of a Canada-wide forensic entomology database being compiled by Dr. Gail S. Anderson at Simon Fraser University. As a result of this research, a list of the insect taxa associated with above ground pig carrion in sunny and shaded areas during three seasons in three rural areas in Manitoba was compiled (Appendix 1).

A minimum of 13 arthropod orders, 61 families and 95 species were collected and identified over the duration of this study. These species included necrophagous species, predators and parasites of necrophagous species and incidental species. Of these, a minimum of 13 families and 37 species from Diptera and Coleoptera used the pig carrion to feed and/or breed for at least a part of their life cycle. Other researchers have shown varying numbers of arthropods collected from different types and sizes of carrion. De Jong and Chadwick (1999) reported a total of 53 arthropod species collected from rabbit carrion at different elevations in Colorado. Payne (1965) reported a total of 522 arthropod species associated with small (1000 – 1400 g) pig carrion in South Carolina. Watson and Carlton (2003) reported 93 arthropod species associated with black bear, deer, alligator, and pig carrion in Louisiana. Early and Goff (1986) reported 133 arthropod species collected from dead cats in O'ahu, Hawaii. Grassberger and Frank (2004) recorded 42 arthropod species collected from pig carrion in an urban area in Europe.

The sequence of arthropods in the sunny and shaded areas of this study followed the same general pattern observed in tropical and temperate areas. The necrophagous flies, primarily the Calliphoridae, Sarcophagidae and Muscidae, predominated in the carcasses; predators of these species such as the Staphylinidae, some Silphidae, Histeridae, Vespidae, and Formicidae began to arrive in the sequence in response to the presence of huge numbers of eggs, larvae and adult flies; and as the carrion decomposed and became more favourable to species that were attracted to the later stages of decay, primarily species in the Silphidae, Piophildae, Cleridae, Nitidulidae and Dermestidae, colonized the carcasses. Anderson and VanLaerhoven (1996), Payne (1965), Early and Goff (1986), Tabor *et al.* (2004) and Grassberger and Frank (2004) observed a number of basic similarities in arthropod succession with major differences being in the arrival sequence of different species within these insect families.

In my study, groups of arthropods involved in the decomposition process or associated with carrion were similar in terms of timing of arrival and duration of stay over the entire decay process between sunny and shaded areas. Differences in species composition between trials were observed; however, it should be noted that seasonal comparisons within this study are difficult since the summer, fall, and spring trials were conducted in three different rural areas in Manitoba. Overall, six species of Calliphoridae were collected from sun-exposed carrion and three species were collected from shade-exposed carrion during the summer trial; three and four species were collected from sun- and shade-exposed carrion, respectively, during the fall trial; and four and seven species were found to occur on sun- and shade-exposed pig carrion

during the spring trial (Appendix 1). *Phormia regina* was the predominant calliphorid species and was represented in sun and shade-exposed carrion in all three trials; and *Lucilia illustris* also occurred in all three areas. *Calliphora vicina* was present exclusively on sun-exposed pig carrion during the summer trial and on shade-exposed carrion in the spring trial; *Calliphora vomitoria* was collected solely during the fall sampling period; *Cynomya cadaverina* were found to only occur during the spring trial; *Phaenicia sericata* was collected during the summer trial on sun-exposed carrion; and *Protophormia terraenovae* were collected in small numbers at all three locations. Payne (1965) showed that *Cochliomyia macellaria* (Fabricius) was the main calliphorid collected from pig carrion during summer in South Carolina. This species was not found in my study, though collected previously in Manitoba (T. D. Galloway, unpublished). Watson and Carlton (2003) reported that *P. regina*, *Phaenica coeruleiviridis* (Macquart) and *Phaenicia sericata* (Meigen) were the dominant calliphorid species during their spring study in Louisiana. Grassberger and Frank (2004) showed that during their spring trial, *C. vomitoria*, *Lucilia* spp., *P. terraenovae* and *P. regina* were the most common calliphorid species collected from pig carrion in central Europe. During the spring study by Tabor *et al.* (2004) in southwest Virginia, *P. regina* were the most common and *C. vicinia* and *C. vomitoria* were also collected; during the summer portion of this study, *P. regina* and P. *coeruleiviridis* was equally abundant and *C. macellaria* was also collected during this time.

In Manitoba, *P. regina* was first to arrive and was the predominant species in sunny and shaded areas during the summer trial. This species was observed within 30 minutes of pig placement. It was also noted that oviposition occurred sooner on the

shade-exposed carrion. *Lucilia illustris* was observed in sun and shade on Day 0 and then not until 20 days after death. Adults of *Calliphora vicina* were collected from sun-exposed carrion only and not until Day 24. Anderson and VanLaerhoven (1996) found that *L. illustris* arrived within minutes and eggs were laid within one hour of death. They also reported that *P. regina* arrived soon after death and did not lay eggs until Day 2. Joy *et al.* (2002) found that *P. regina* was the dominant species throughout May and confirmed other reports that this species is a common spring species. Watson and Carlton (2003), found *P. regina* was the latest calliphorid species to arrive on swine in their spring study (Day 3) and by Day 4 was either the only species or the dominant species at all sites. Contrary to other research, in which there was a distinct seasonal difference in blow fly species (Hall 1948; Hall and Doisy 1993; Introna *et. al* 1991; Tessmer and Meek 1996), *P. regina* was strongly represented as adult and larvae during all three seasons in Manitoba. *Calliphora vomitoria*, *L. illustris* and *P. regina* were collected within the first day of pig placement in sun and shade during the fall trial. *Phormia regina*, *L. illustris* and *C. cadaverina* were all observed within the first three days of pig placement during the spring trial, while *P. terraenovae* which was not seen on the shade-exposed carrion until 9 days after death. Furthermore, Bourel *et al.* (1999) found a considerable difference in blow fly colonization of rabbit carrion from one year to the next in the same location and during the during sample period. In 1996, they showed *C. vicina* and *C. vomitoria* were the first species to colonize the spring-exposed carcasses. However, these species did not arrive until day three and did not lay eggs until day five. In the following year, the carrion was exposed during the same time period and *C. vicina* and *C. vomitoria* were seen actively laying eggs on the first day of

exposure. From my study, it appears that previously reported conclusions that certain calliphorid species are more prevalent and active during different seasons may be overgeneralizations.

In all three trials, adult Piophilidae were collected much earlier than larvae were observed. During the summer trial, *S. nigriceps* and *P. xanthostoma* were present on sun and shade-exposed carrion only six days after death, while larvae were not observed until 62 days after death in the sun and 30 days after death in the shade. This observation was most consistent with Anderson and VanLaerhoven (1996), where piophilid larvae were collected as early as 29 days after death. Similarly, in my study, during the fall trial piophilid larvae were apparent 26 days after death and up to 41 days after death during the spring trial. Furthermore, collections of insects after the winter period I found that piophilids over-wintered as late instar larvae.

Three species of silphids were collected during the summer trial; six species were collected during the fall trial; and ten species were collected from shaded pig carrion during the spring trial. Adult and larval *Oiceoptoma noveboracensis* and *Necrodes surinamensis* were collected early in the decay process during the summer and spring trials, but not until much later during the fall trial. Other researchers have recorded silphids arriving both early and later in the decay process (Anderson and VanLaerhoven 1996; Payne and King 1970; Tabor *et al.* 2004). As a result, I concluded that the presence of these beetles was strongly attributed to life history and are not reliable indicators in forensic studies.

Creophilus maxillosus (Linnaeus) and *Ontholestes cingulatus* (Gravenhorst) (Staphylinidae) were the most obvious predators of Diptera larvae associated with

carrion. These species were apparent within the first eight days after death during the summer and spring trial. They were not recorded until 269 days after death during the fall trial (i.e., in the spring), with the exception of *C. maxillosus*, which occurred on shade-exposed carrion 22 days after pig placement. It has been well documented that staphylinids occur throughout the decay process (Anderson and VanLaerhoven 1996; Payne and King 1970; Watson and Carlton 2003). From my findings, I assumed that the arrival and presence of these species of Staphylinidae were a function of life history and are not reliable indicators in forensic studies. An attempt was made to collect and identify all adult staphylinids for the duration of all three trials. Unfortunately, this was not possible since the diversity was vast and the taxonomic expertise necessary was too great. However, I collected at least 32 different species of staphylinids recorded to occur on sun and shade-exposed carrion during the summer trial. Payne and King (1970) found more than fifty species of Staphylinidae that were present throughout the decay process.

Adult *Necrobia rufipes* and *N. violacea* occurred during the decay stage, but larvae were not collected until later in the advanced decay stage during the summer and spring trials. Adult and larval *N. violacea* were present later in the advanced decay stage during the fall trial. These findings were consistent with other research. For instance, Grassberger and Frank (2004) found adult *N. rufipes* and *N. violacea* were present as early as the bloat stage during their spring and summer trials and larvae were not present until later in the decay stage. Similarly, Anderson and VanLaerhoven (1996) found adults to occur early in decomposition. However, Payne and King (1970) did not find the larvae until the dry/remains stage.

Adult nitidulids (*Nitidula ziczac* Say) were first collected six days after death on shade-exposed carrion and 24 days after death on sun-exposed carrion during the summer trial. Similarly, this species was collected 33 days after death on sun-exposed carrion and nine days after death from shade-exposed carrion during the spring trial. This was consistent with Anderson and VanLaerhoven (1996) that reported this species occurred sooner in the decay process. However, this species was not present in the fall trial until 258 days after death (i.e, in the spring), which proved consistent with Payne and King (1970), who reported that this species feeds on moist skin and is found later in the decay process, commonly found associated with the dry stages.

Adult and larval Dermestidae were present during the later stages of advanced decay. Anderson and VanLaerhoven (1996) collected larvae as early as 21 days after death; dermestids were commonly collected 43 days after death in their study. These beetles are considered most common in the dry remains stage (Grassberger and Frank 2004; Payne and King 1970); however, during the fall trial, I found adult *D. lardarius* as early as four days after death.

One species of Trogidae (*Trox unistriatus*) was common to all three trials and was most common in the later stages of advanced decay for the summer and fall trials. Trogidae are commonly associated with drier carrion. Payne and King (1970) recorded eight species present on pig carrion in the advance decay and remains stage and stated that all species were found feeding on dried carrion. However, during the spring trial, I found adults as early as nine days after death. The presence of these beetles so early in the decay process might be a function of peak seasonal appearance rather than the decompositional state of the carrion.

Geotrupes semiopacus (Geotrupidae) occurred throughout the fresh, bloat, decay, and advanced decay stages on shaded pig carrion during the fall and spring trials. Payne (1965) reported that this group first occurred in the active decay stage. Because these beetles construct tunnels for larval rearing, they are typically found in areas with less dense soil types. No species of Geotrupidae were found during the summer trial at Glenlea Research Station. It was assumed that since clay soils predominate at Glenlea, these beetles are not typical of this area.

Vespidae (*Dolichovespula* sp. and *Vespula* sp.) and Formicidae were significant predators of fly eggs, larvae and adults during all trials and regardless of habitat, which is consistent with previous findings (Anderson and VanLaerhoven 1996; Early and Goff 1986; Payne 1965).

A complete list of the species of Histeridae present on sun and shade-exposed carrion was compiled for the spring trial (Appendix 1). Throughout decomposition, thirteen species were collected from sun-exposed carrion and seven species occurred on shaded carrion. Payne and King (1970) reported 28 species of histerids from carrion collected at various times during four years of research; however, Anderson and VanLaerhoven (1996) reported that only one species was collected from soil samples during the dry remains stage in British Columbia.

During the spring trial, nineteen species of carabids were collected from sun-exposed carrion and 14 species were collected from shaded carrion throughout the decay process (Appendix 1). The role of carabids as predators of carrion insects is considered minor (Payne and King 1970); however, the role they play in carrion ecology has been generally ignored.

A minimum of four genera of Shaeroceridae was recorded from sun and shade-exposed carrion during decay and advanced decay in the spring trial; only two of which were recorded to occur during the dry remains stage as described in Anderson and VanLaerhoven (1996). Sepsidae, Drosophilidae, and Acarina were numerous and were not taken beyond the family level; however, more attention is necessary to understand the role of these groups of insects in the succession.

Observations of decomposition and insect colonization on 22, 70kg pig carcasses lasted from immediately after death until more than 14 months after death during the summer trial, 12 months after death during the fall trial and 11 months after death during the spring trial. These studies were carried out over the longest period ever reported. Anderson and VanLaerhoven (1996) monitored 22kg pig carcasses for more than nine months after death in an open, sunlit, rural area in southwestern British Columbia. Early and Goff (1986) and Tullis and Goff (1987), used small carrion in tropical areas and reported that insect colonization lasted up to three months after carcass placement. Even in more temperate areas, Payne (1965) showed that insect colonization time on small pig carrion was completed within four weeks. In Colorado, De Jong and Chadwick (1999) studied the decomposition and arthropod succession of rabbit carrion (mean 1.62kg) at various elevations and recorded insect colonization for a total of 51-days. In Louisiana, Watson and Carlton (2003) studied the spring succession of arthropods and recorded insect activity on deer and swine until two months after carcass placement.

The differences in rate of decomposition and resultant insect colonization are likely due to geographic location and size of carrion. Carcass type and size can have

an effect on the decomposition rate and insect succession (Anderson and VanLaerhoven 1996). A frequent concern has been the validity of the use of these data for comparison as the baseline in forensic entomology cases (Catts and Goff 1992). Kuusela and Hanski (1982) showed that large carrion does not attract more carrion flies or species of flies and there is a positive relationship between the size of carrion and the numbers of flies bred. However, Catts and Goff (1992) noted that in 1989, Haskell found that the rate of decomposition was a function of the amount of carrion present and that an adult human and pig took three to five times longer to decompose to skeletal remains than an infant corpse.

During my study, it was important to approximate closely the process of decomposition more thoroughly for a mean adult human. Therefore, 70kg pig carcasses were used as human models to study decomposition and insect succession. As a consequence, there were enormous numbers of insects to contend with, especially during the peak maggot period for each seasonal trial. For example, during the summer trial, an estimated minimum of 11,792 maggots were collected from two sun-exposed pig carcasses and 70,994 maggots from two shaded pig carcasses. During the fall trial, pitfall traps captured an estimated minimum of 30,183 maggots from two sun-exposed pig carcasses and 39,051 maggots from two shaded pig carcasses over a five-week period. Approximately 90% of the total maggots captured were collected during the second week of pig placement. There did not appear to be a directional bias for the movement of maggots captured in the four cardinal pitfall traps. However, maggots were captured in the pitfall trap furthest away, which indicated the potential for maggots

to move at least 15m away from a corpse. In addition, it was observed that maggots moved into a hollow tree branch 1m aboveground.

Furthermore, each trial had an over-winter period to simulate actual conditions that a body would experience when left to decompose in this province. Manitoba is under winter conditions for the majority of the year and a widespread temperature range of plus 30C and minus 30C throughout a year is common. For a significant period of time, insects are in an over-wintering state and therefore are assumed to not be actively feeding and/or breeding on carrion.

In the summer trial, I observed that the start of the first two stages of decomposition occurred concurrently in the sunny and shaded areas. However, in the shade the bloat stage was longer by two days. In the decay and advanced decay stages, there was also a two-day lag in carrion decomposition in the shaded area. It was also shown that biomass loss was slightly slower in the shade during this point in time; however, there was no significant difference in the rate of biomass loss in sun and shade-exposed carrion. In the fall trial, both the fresh and bloat stages were the same length of time; however, the decay stage was faster in the sunny area than in the shaded area. The movement of the calliphorid maggots away from the pig carcasses marked the change from the decay to the advanced decay stage. Therefore, the calliphorid maggots entered the prepupal stage sooner on the sun-exposed carrion. The most obvious difference in rate of decay between sun and shade-exposed pig carrion was observed during the spring trial, where all stages of decomposition took longer in the shade-exposed carrion. During this trial, the rate of biomass loss was much more dramatic in the sun-exposed carcasses after Day 6.

Once all maggot activity ceased, it was assumed that the advanced decay stage was complete and the dry remains stage had stage begun. However, it was observed that the distinction between the advanced decay and dry remains stage was difficult to differentiate and fluctuated depending on rainfall and humidity. There were several instances when it looked like the carcasses were beginning to enter the dry remains stage and the insect activity was diminishing; but following periods of rain, insect activity would resume. Payne (1965) also noted that rain caused a “partial repetition of succession” and some species attracted to the advanced decay stage were attracted to these wet remains. Therefore, a discrete stage of decay immediately following the advanced decay stage was not obvious. For this same reason, it was also observed that there was no distinct end point for the dry remains stage. This was consistent with findings from Payne (1965) and Early and Goff (1986), who also failed to indicate a definitive end for the final stages of decomposition. In both studies, the dry and the remains stages were described separately and the dry stage began when the carcass consisted of only dry skin, cartilage, and bones, and internal temperature began to track ambient temperature. The remains stage began when only bones and bits of fur remained and no carrion-feeding arthropods were found. However, in both studies, the final stages of decomposition were difficult to define in accordance with their generalizations. Decomposition is a continuous process without discrete stages (Schoenly and Reid 1987). However, many researchers have divided this process into four to six stages (Lord and Burger 1984; Payne 1965; Tantawi *et al.* 1996; Turner 1991). With respect to the number of identifiable decompositional stages, I showed that at least four stages are apparent. Based on the physical state of the carcass, internal

temperature and insect activity, the distinction between fresh, bloat decay and advanced decay were obvious and most similar to those described by Anderson and VanLaerhoven (1996).

Overall, the internal carcass temperatures were higher than corresponding ambient air temperatures in both sunny and shaded areas. As shown in other studies, the high internal carcass temperatures were directly related to the heat generated from the activity of maggots within masses (Catts 1992; De Jong and Chadwick 1999; Joy *et al.* 2002; Payne 1965). In the summer trial, I found that the internal carcass temperature was similar for sun-exposed and shaded pig carrion, indicating that the ambient air temperature had no effect on maggot mass temperature. Maximum internal carcass temperatures reached 37.6C in the shade-exposed carrion and 36.7C in the sun-exposed carrion. Corresponding ambient temperatures were 24.3C and 27.9C, in shade and sun areas, respectively. The sunny and shaded conditions seemed to affect the rate of insect development during the summer trial and this was observed for *P. regina*. There was a distinct lag in the development time for *P. regina* collected from shade-exposed pig carrion. Teneral adults were observed sooner on the sun-exposed pig carrion, and teneral adults were present and emerging for a longer period of time from shade-exposed carrion. This was similar to Joy *et al.* (2002) who compared the larval activity on sunlit and shaded raccoon carrion for a 153-h period during the spring in southwestern Virginia. They determined that the maggot mass temperatures in sun- and shade-exposed carrion were the same; however, the mean developmental times for *P. regina* larvae collected from sun-exposed carrion were greater than mean developmental times for larvae in shaded carrion. There was an increase in the growth

and activity of maggots on sun-exposed carrion, thereby affecting maggot developmental times. During the fall trial, the delay in calliphorid development was not apparent in sun versus shaded conditions. Development and emergence of the progeny of first generation *P. regina* on sun- and shade-exposed pig carrion was observed during the same time period. This could be due to ambient temperatures in sunny and shaded areas being more similar than mean temperatures measured during the summer trial. Similarly, in the spring trial there was no apparent difference in the rate of development of calliphorid larvae within sunny and shaded areas. However, it is likely that this is the result of the developing calliphorid larvae being exposed to cooler overnight conditions, regardless of shade or sun exposure.

I have provided valuable baseline information on the necrophages, their timing of arrival and other species associated with sun- and shade-exposed pig carrion in three rural areas in Manitoba. However, making direct comparisons from other field studies of this nature are often difficult because of differences in the numbers, type and size of carrion used, insect sampling techniques, intensity and frequency, conditions such as sun-exposure, climate, season and geographic location. Furthermore, due to the need for a wide variety of taxonomic expertise, there is a tendency to report only a portion of the insects found on carrion based on the insect taxa previously published as forensically significant, based on bias towards large, easily collected arthropods and based on the taxonomic difficulty of some groups (i.e., Acarina, Sphaeroceridae, Sepsidae, Histeridae, Drosophilidae, Piophilidae and many Staphylinidae).

The estimation of a postmortem interval involves setting a probable minimal and maximal time period from death to the discovery of a corpse. Analyzing the insect

species present can be used to estimate the maximum time between death and discovery of a corpse. Similarly, the age of developing immature insects at the time of corpse discovery can be estimated to determine the minimum amount of time lapsed since time of death. Analysis and inferences of these data are based on published baseline studies and developmental rates are adjusted to take into account the influence of conditions such as location, temperature and season (Catts 1992). Accurate postmortem intervals are paramount because the number of possible suspects may be reduced in homicide and other questionable death situations and can aid in the possible identification of the deceased (Catts 1990; Catts 1992; Schoenly *et al.* 1996). However, the certainty of the postmortem intervals derived from succession-based insect data has been criticized for its lack of statistical confidence (Schoenly 1992; Schoenly *et al.* 1992; Schoenly *et al.* 1996; Schoenly and Reid 1987). For this reason, we need more preliminary ecological studies rather than studies that focus on the specifics of applied forensic information. Since there are many factors that can affect the timing of arrival and species composition of carrion fauna, there is a need for more research related to species composition in different geographical regions throughout North America. Furthermore, these geographical studies need to be performed in a variety of habitats, under varied conditions, with an increased emphasis on the taxonomy, biology and ecology of carrion arthropods for entomology to be maintained as a reliable method to estimate postmortem intervals.

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Figure 1. Caged pig carcass illustrating the sunny area. This photograph was taken at Elm Creek, MB at the start of the spring trial (29 May, 1999).

Figure 2. Caged pig carcass illustrating the shaded area. This photograph was taken on Day 2 (31 May, 1999) at Elm Creek, MB during the spring trial.

Figure 3. Steel cages used to protect pig carcasses from vertebrate scavengers at Glenlea Research Station and Sandilands Provincial Forest. This photograph was taken at Sandilands Provincial Forest during the fall trial.

Figure 4. Arrangement and classification of sampled (A, B, C and D) and unsampled (Ec, Fc, Gc and Hc) pig carcasses in sunny and shaded areas at Glenlea Research Station, Sandilands Provincial Forest and Elm Creek. Insects associated with pig carcasses A, B, C and D were collected via sweep net, hand-picking and pitfall traps. Insects associated with pig carcasses Ec, Fc, Gc and Hc were not collected.

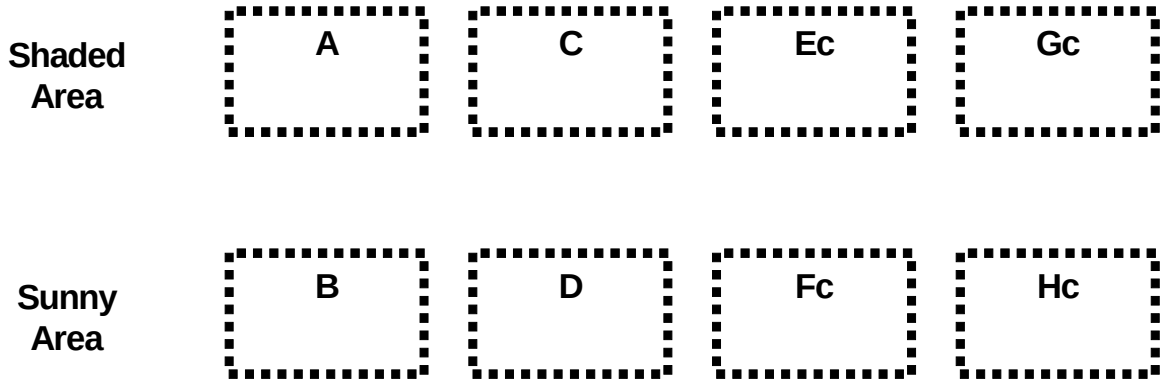


Figure 5. Sample methods used to collect insects from pig carcasses at Glenlea Research Station, Sandilands Provincial Forest and Elm Creek. (A. Aspirator; B. Hand-pick; C. Sweep net)

A.

B.

C.

Figure 6. Arrangement of pitfall traps around each pig carcass at Glenlea Research Station, Sandilands Provincial Forest and Elm Creek. All plots were 2m x 18m and a distance of at least 50m separated each carcass.

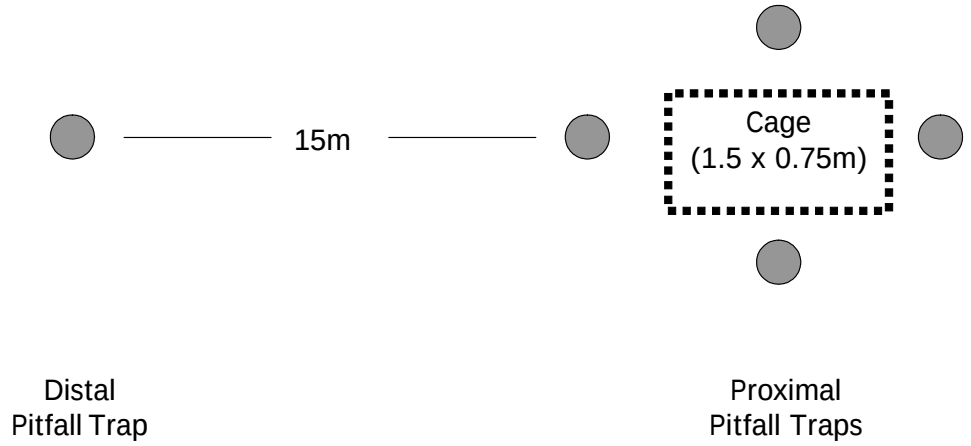


Figure 7. The orientation of a pitfall trap relative to a caged pig carcass (A) and one pitfall trap showing its placement, wooden cover and trap capture of maggots during a one-week period (B).

A.

B.

Figure 8. HOBO® temperature data logger probe inserted into knife wound of pig thorax to measure internal carcass temperature of pig carrion in sunny and shaded areas at Glenlea Research Station, Sandilands Provincial Forest and Elm Creek.

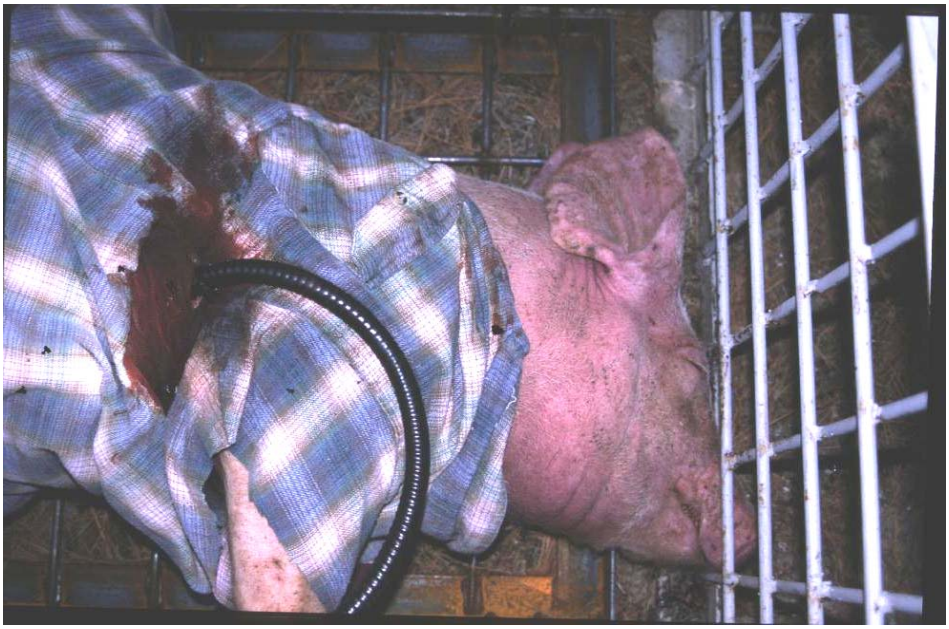


Figure 9. HOBO® temperature data logger situated approximately 1m above ground to measure the ambient air temperature in sunny and shaded areas at Glenlea Research Station, Sandilands Provincial Forest and Elm Creek.

Figure 10. Tripod and scale used to measure pig carrion biomass loss over time in sunny and shaded areas at Glenlea Research Station and Elm Creek.

Figure 11. Time of arrival and duration of stay of the adult Calliphoridae collected from pig carrion in sunny and shaded areas at Glenlea Research Station. The slash marks denote the winter period (//). (Start date: 30 June 1998; Winter period: 01 October, 1998 – 14 May, 1999; End date: 01 September, 1999)

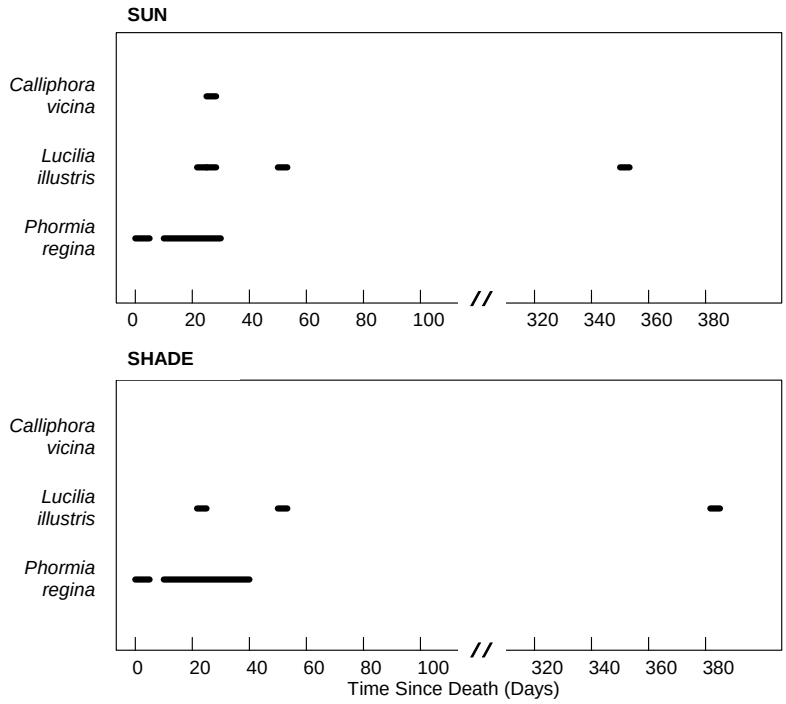


Figure 12. Time of arrival and duration of stay of the adult and larval Piophilidae collected from pig carrion in sunny and shaded areas at Glenlea ResearchStation. The slash marks denote the winter period (//). (Start date: 30 June 1998; Winter period: 01 October, 1998 – 14 May, 1999; End date: 01 September, 1999

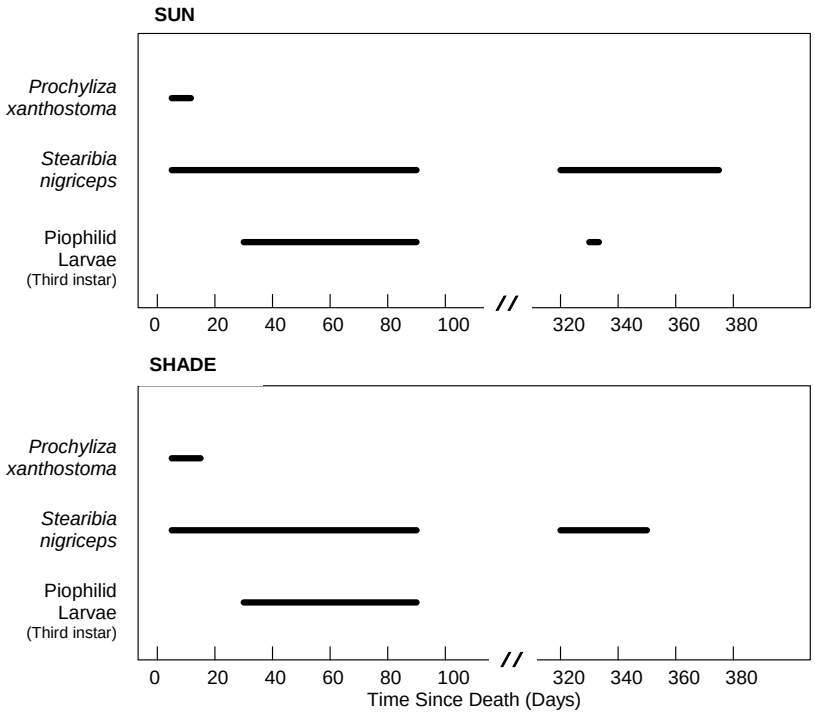


Figure 13. Time of arrival and duration of stay of the adult and larval Silphidae collected from pig carrion in sunny and shaded areas at Glenlea Research Station. The slash marks denote the winter period (//). (Start date: 30 June 1998; Winter period: 01 October, 1998 – 14 May, 1999; End date: 01 September, 1999)

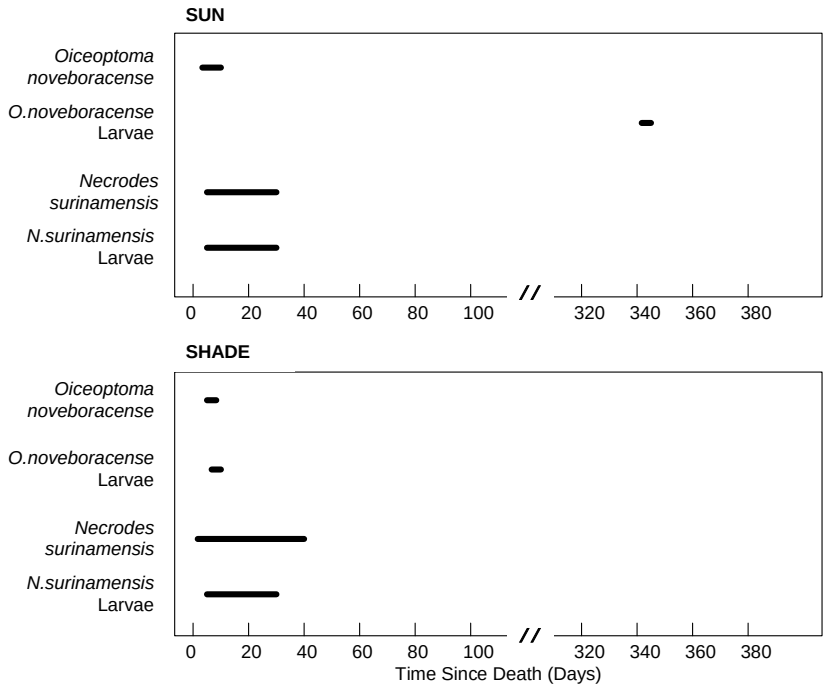


Figure 14. Time of arrival and duration of stay of the adult Staphylinidae collected from pig carrion in sunny and shaded areas at Glenlea Research Station. The slash marks denote the winter period (//). (Start date: 30 June 1998; Winter period: 01 October, 1998 – 14 May, 1999; End date: 01 September, 1999)

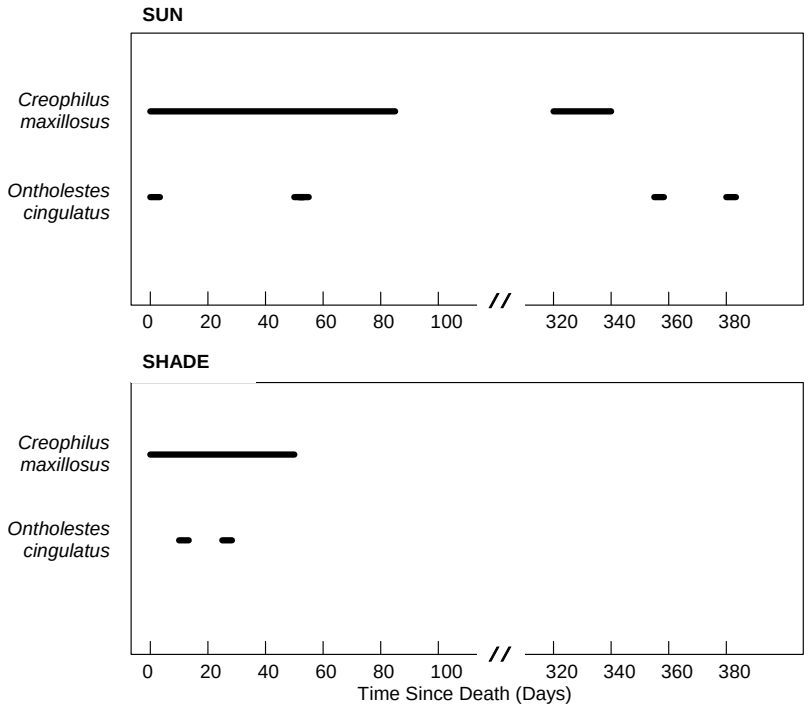


Figure 15. Time of arrival and duration of stay of the adult Cleridae collected from pig carrion in sunny and shaded areas at Glenlea Research Station. The slash marks denote the winter period (//). (Start date: 30 June 1998; Winter period: 01 October, 1998 – 14 May, 1999; End date: 01 September, 1999)

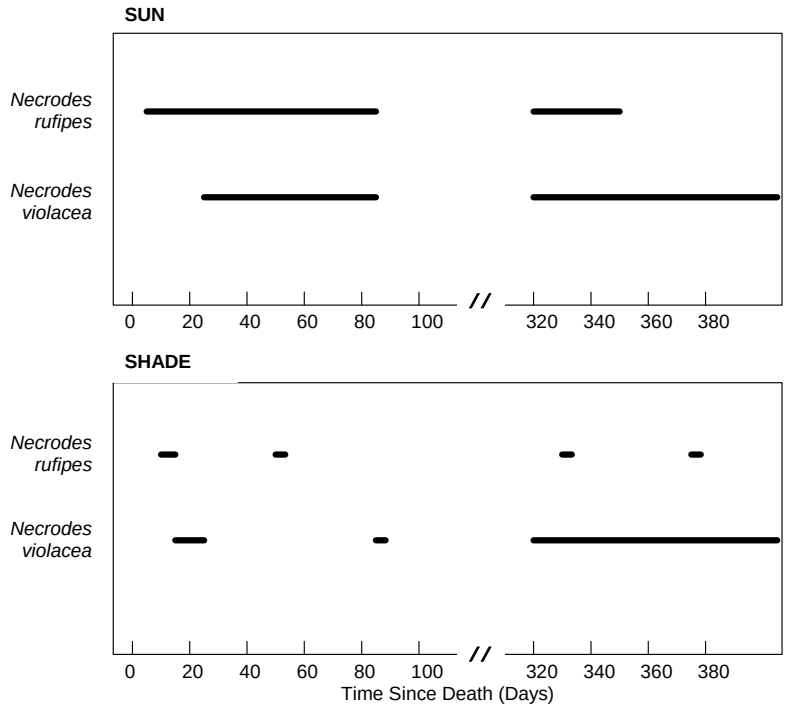


Figure 16. Time of arrival and duration of stay of the adult Nitidulidae and Dermestidae collected from pig carrion in sunny and shaded areas at Glenlea Research Station. The slash marks denote the winter period (//). (Start date: 30 June 1998; Winter period: 01 October, 1998 – 14 May, 1999; End date: 01 September, 1999)

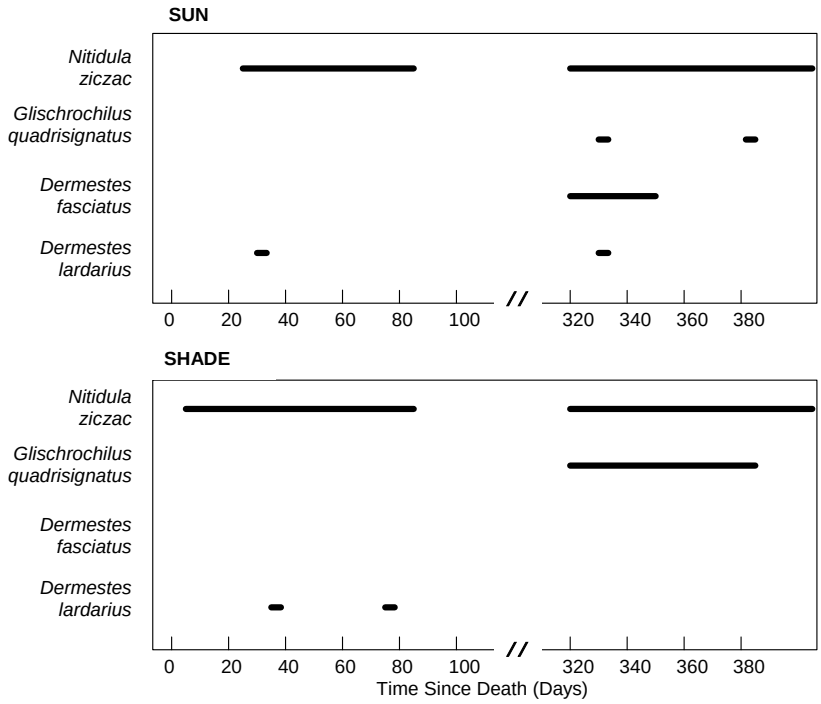


Figure 17. Time of arrival and duration of stay of the adult Trogidae and Geotrupidae collected from pig carrion in sunny and shaded areas at Glenlea Research Station. The slash marks denote the winter period (//). (Start date: 30 June 1998; Winter period: 01 October, 1998 – 14 May, 1999; End date: 01 September, 1999)

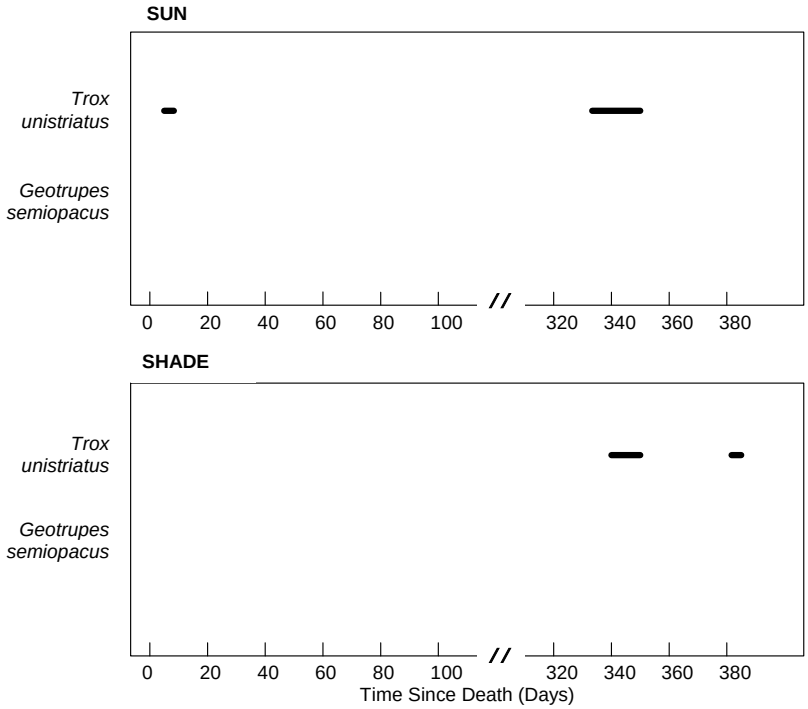


Figure 18. The duration of each stage of decomposition (in days) of pig carrion in sunny and shaded areas during the summer trial at Glenlea Research Station. The slash marks denote the winter period (//).

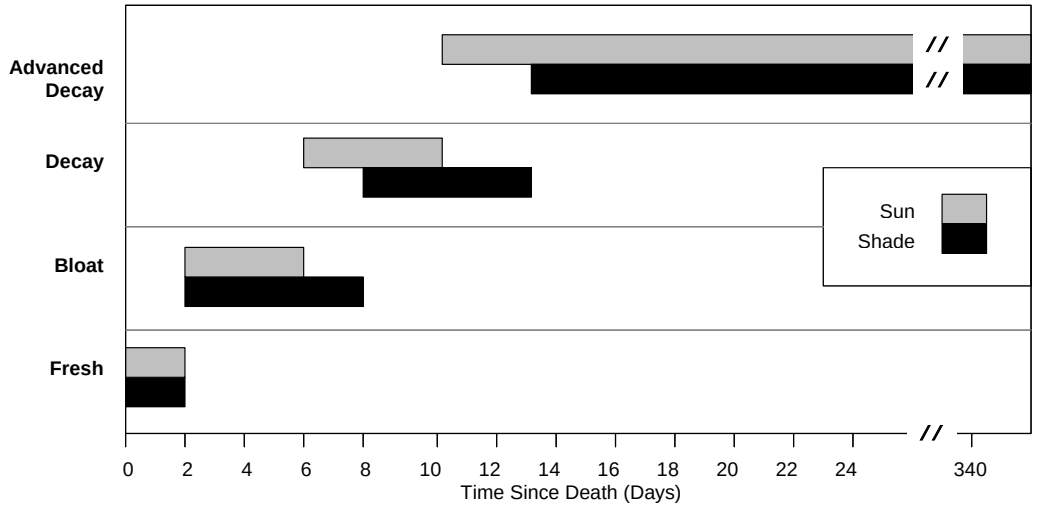
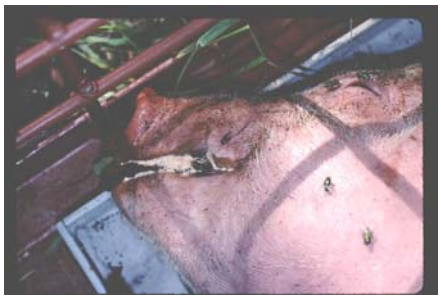


Figure 19. Photographs illustrating the invasion of calliphorids on pig carrion during the summer trial at Glenlea Research Station.

A.



B.

C.

D.

Figure 20. A series of photographs illustrating the stages of decomposition of pig carrion during the summer trial at Glenlea Research Station.

A. Fresh

B. Bloat

C. Decay

D. Decay

E. Advanced Decay

F. Dry Remains

Figure 21. The mean (±SE) biomass of pig carrion over time measured in kilograms in sunny and shaded areas at Glenlea Research Station (n=3).

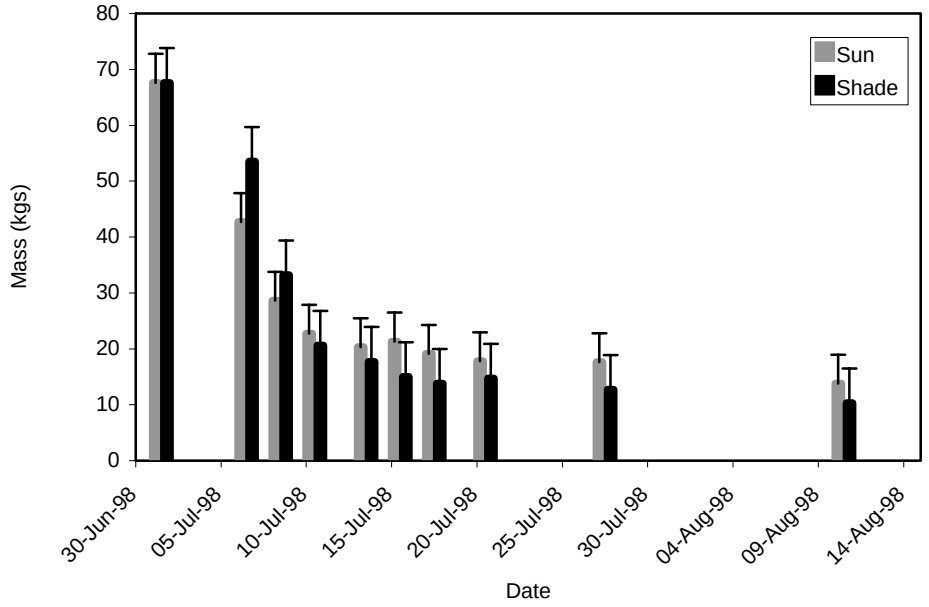


Figure 22. Average daily ambient air and internal carcass temperatures in the sunny area during the summer trial at Glenlea Research Station.

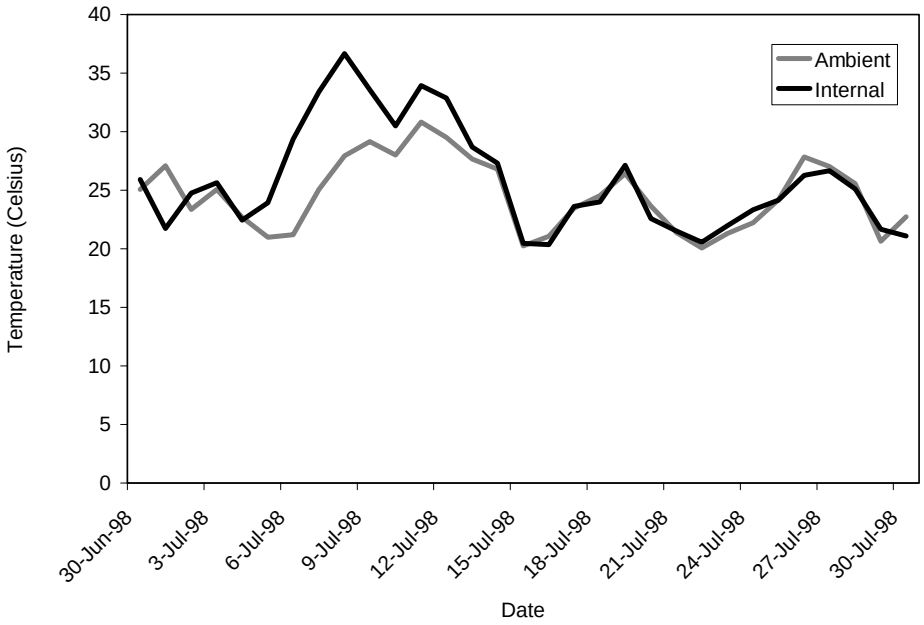


Figure 23. Average daily ambient air and internal carcass temperatures in the shaded area during the summer trial at Glenlea Research Station.

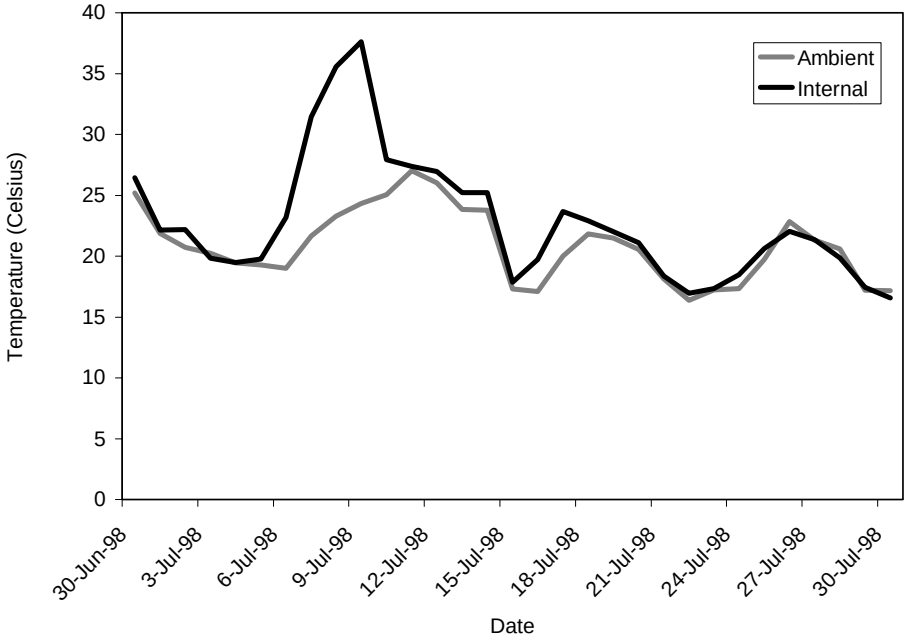


Figure 24. Time of arrival and duration of stay of the adult Calliphoridae collected from pig carrion in sunny and shaded areas at Sandilands Provincial Forest. The slash marks denote the winter period (//). (Start date: 29 August, 1998; Winter period: 01 October, 1998 – 13 May, 1999; End date: 31 August, 1999)

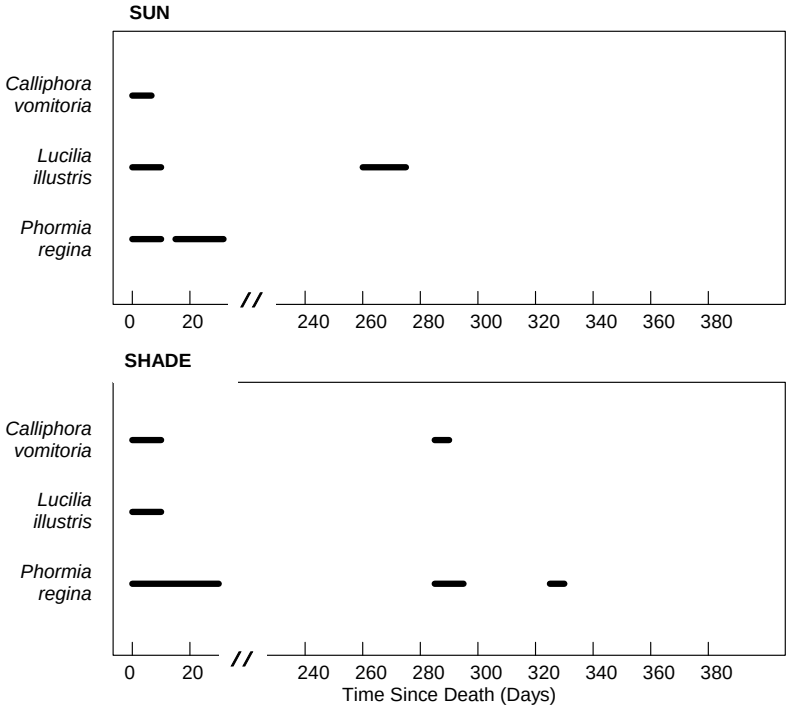


Figure 25. Time of arrival and duration of stay of the adult and larval Piophilidae collected from pig carrion in sunny and shaded areas at Sandilands Provincial Forest. The slash marks denote the winter period (//). (Start date: 29 August, 1998; Winter period: 01 October, 1998 – 13 May, 1999; End date: 31 August, 1999)

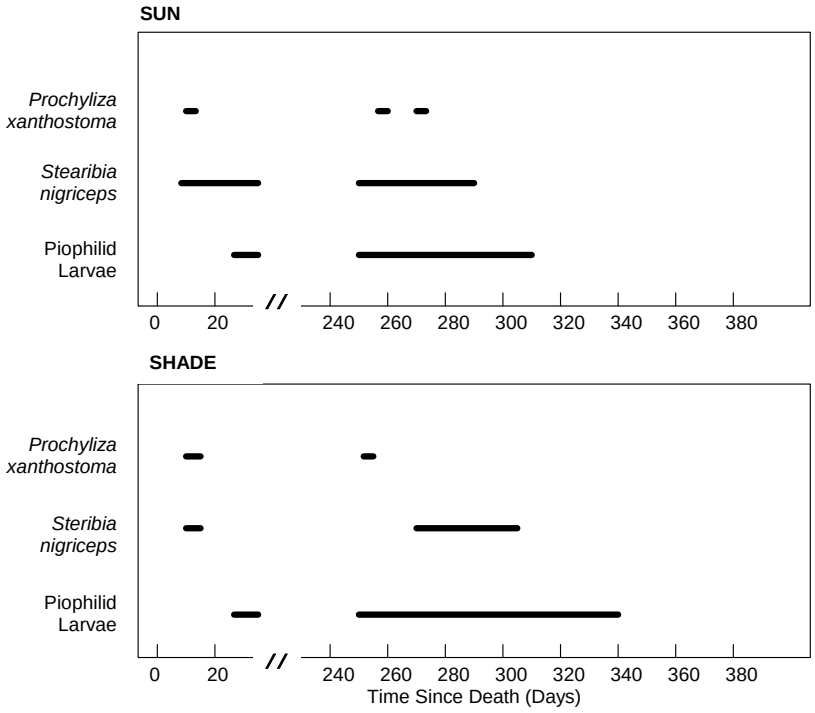


Figure 26. Time of arrival and duration of stay of the adult and larval Silphidae collected from pig carrion in sunny and shaded areas at Sandilands Provincial Forest. The slash marks denote the winter period (//). (Start date: 29 August, 1998; Winter period: 01 October, 1998 – 13 May, 1999; End date: 31 August, 1999)

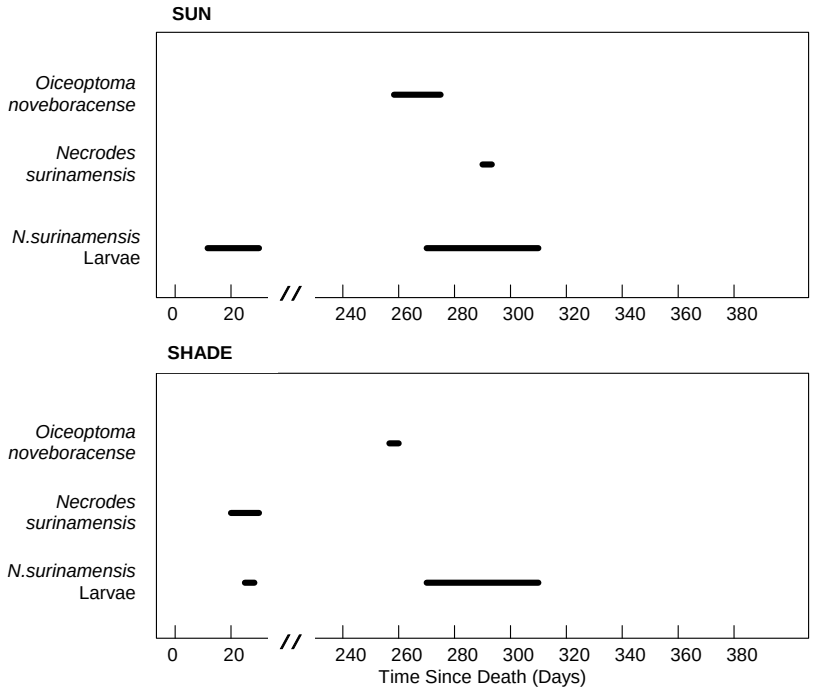


Figure 27. Time of arrival and duration of stay of the adult Staphylinidae collected from pig carrion in sunny and shaded areas at Sandilands Provincial Forest. The slash marks denote the winter period (//). (Start date: 29 August, 1998; Winter period: 01 October, 1998 – 13 May, 1999; End date: 31 August, 1999)

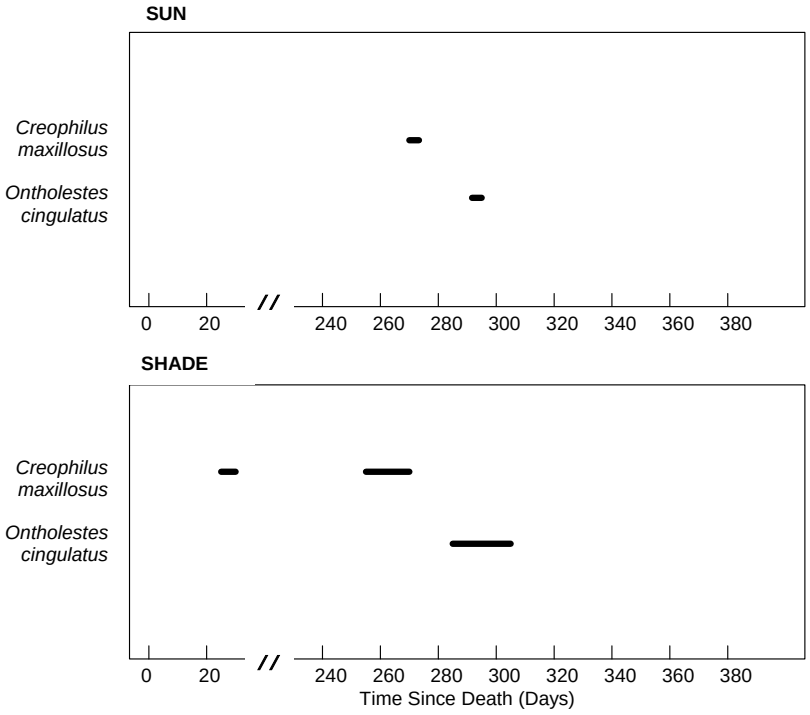


Figure 28. Time of arrival and duration of stay of the adult Cleridae collected from pig carrion in sunny and shaded areas at Sandilands Provincial Forest. The slash marks denote the winter period (//). (Start date: 29 August, 1998; Winter period: 01 October, 1998 – 13 May, 1999; End date: 31 August, 1999).

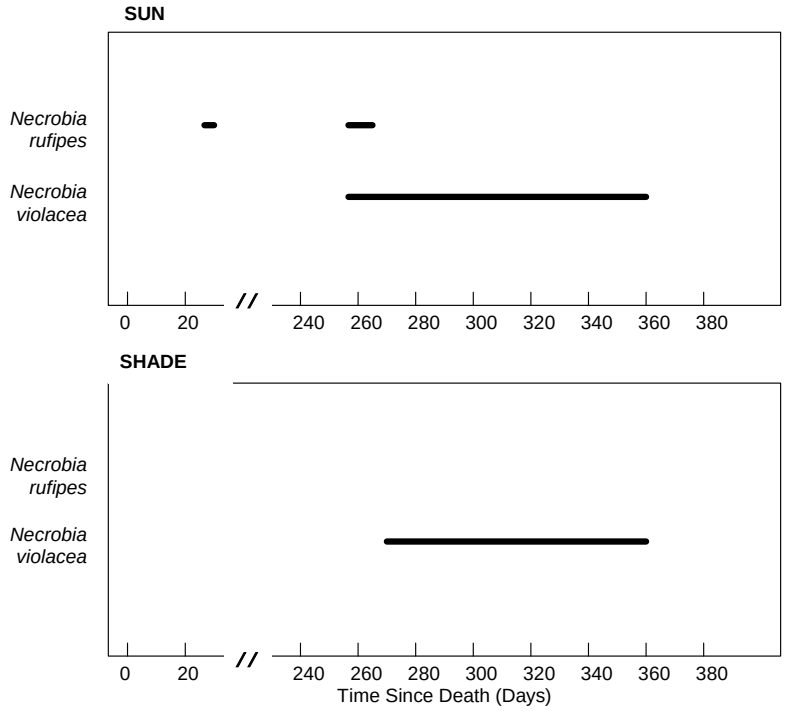


Figure 29. Time of arrival and duration of stay of the adult Nitidulidae and Dermestidae collected from pig carrion in sunny and shaded areas at Sandilands Provincial Forest. The slash marks denote the winter period (//). (Start date: 30 June 1998; Winter period: 01 October, 1998 – 14 May, 1999; End date: 01 September, 1999)

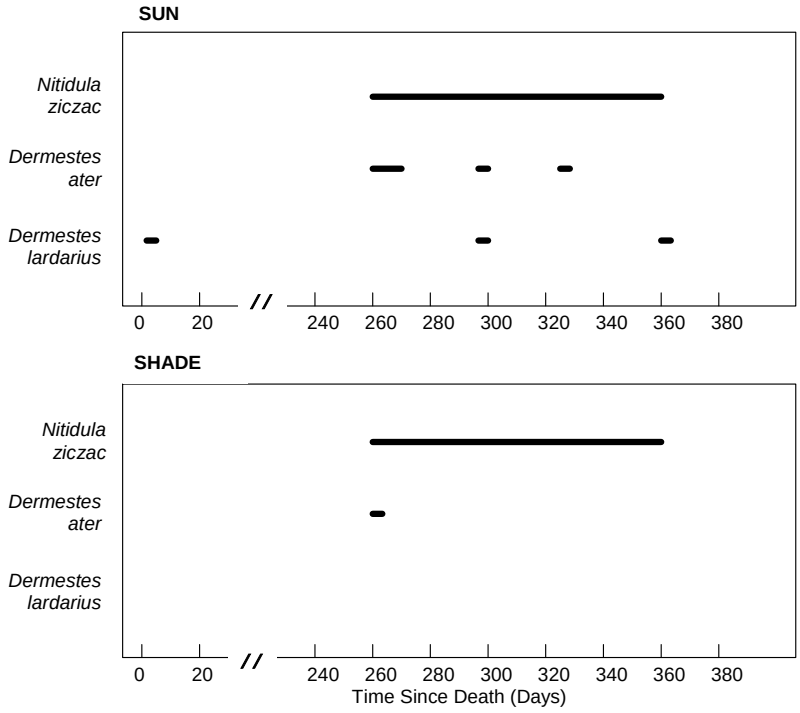


Figure 30. Time of arrival and duration of stay of the adult Trogidae and Geotrupidae collected from pig carrion in sunny and shaded areas at Sandilands Provincial Forest. The slash marks denote the winter period (//). (Start date: 29 August, 1998; Winter period: 01 October, 1998 – 13 May, 1999; End date: 31 August, 1999)

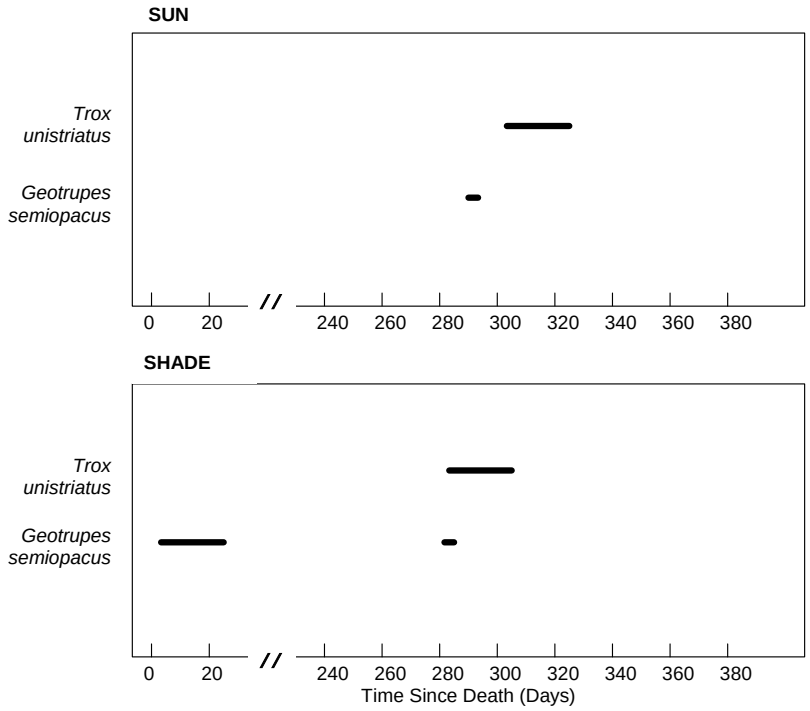


Figure 31. The duration of each stage of decomposition (in days) of pig carrion in sunny and shaded areas during the fall trial at Sandilands Provincial Forest. The slash marks denote the winter period (//).

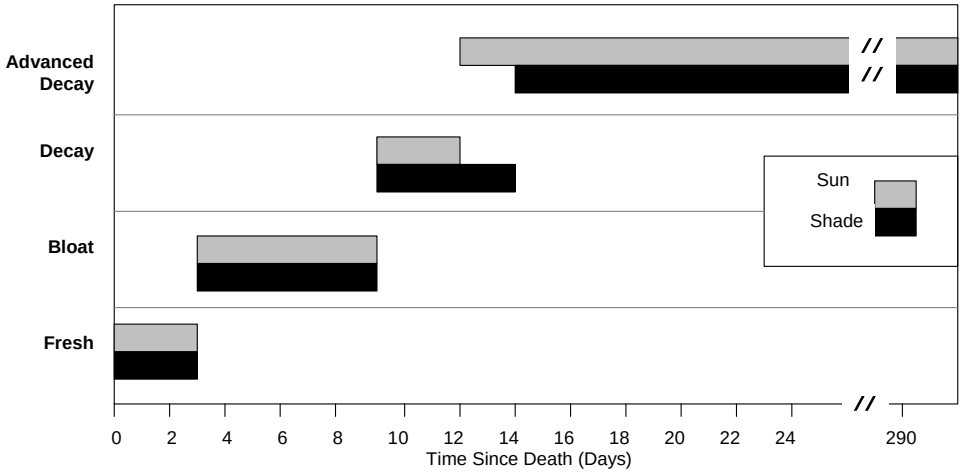


Figure 32. Photographs showing the gravesite of pig carcass (A) and the invasion of calliphorids on pig carrion (B and C) during the fall trial at Sandilands Provincial Forest.

A.

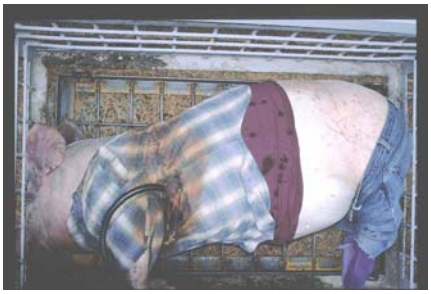
B.

C.

Figure 33. A series of photographs illustrating the stages of decomposition of pig carrion during the fall trial at Sandilands Provincial Forest

A. Fresh

B. Bloat



C. Decay

D. Decay

E. Advanced Decay

F. Dry Remains

Figure 34. Average daily ambient air temperature in the sunny area during the fall trial at Sandilands Provincial Forest.

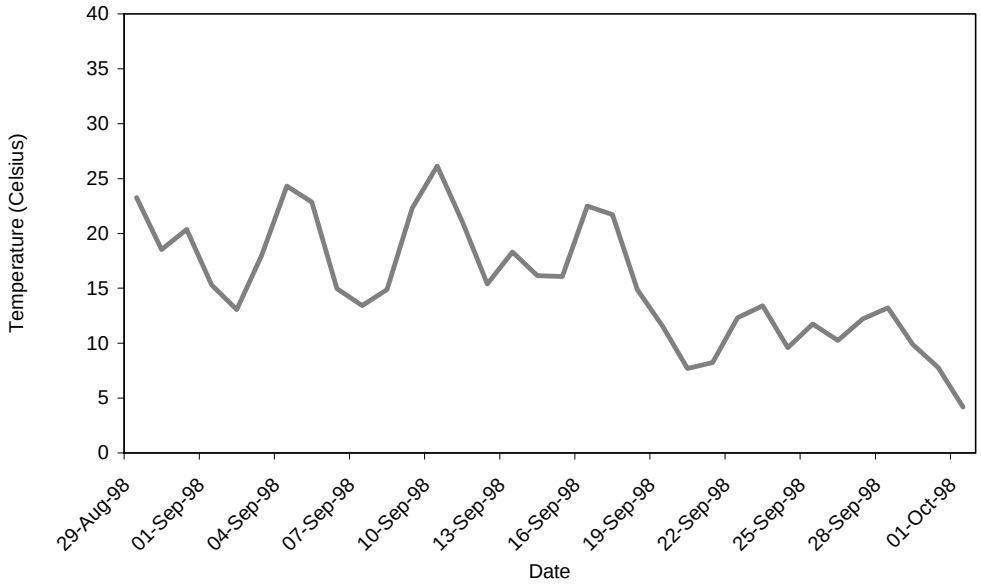


Figure 35. Average daily ambient air temperature and internal carcass temperatures for three pigs (A, Ec and Gc) in the shaded area during the fall trial at Sandilands Provincial Forest.

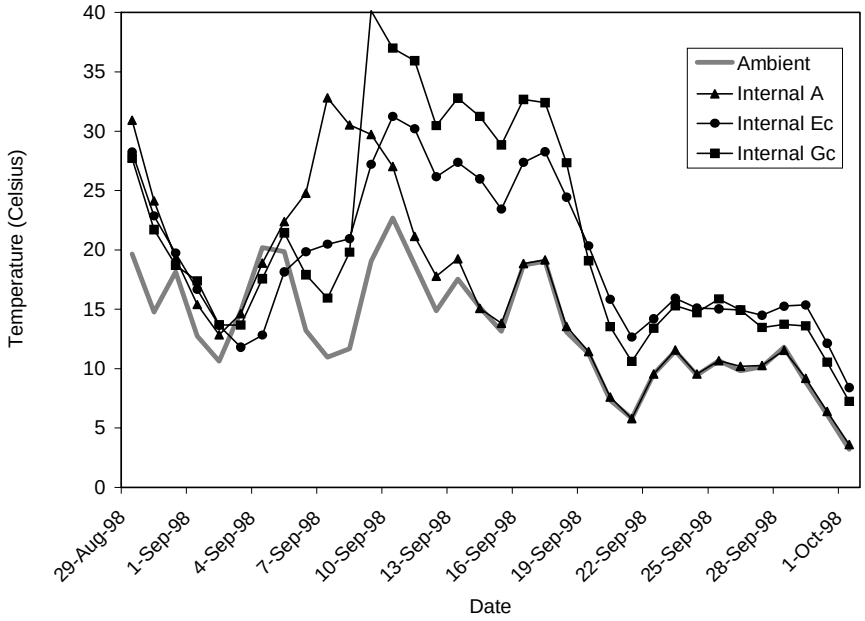


Figure 36. Time of arrival and duration of stay of the adult Calliphoridae collected from pig carrion in sunny and shaded areas at Elm Creek. The slash marks denote the winter period (//). (Start date: 29 May, 1999; Winter period: 02 November, 1999 – 01 May, 2000; End Date: 15 May, 2000)

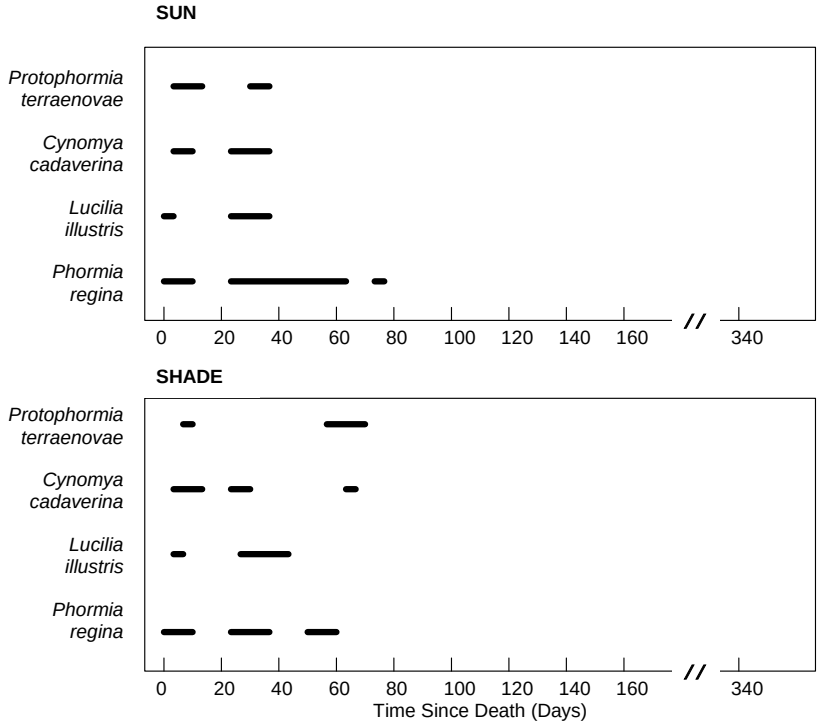


Figure 37. Time of arrival and duration of stay of the adult and larval Piophilidae collected from pig carrion in sunny and shaded areas at Elm Creek. The slash marks denote the winter period (//). (Start date: 29 May, 1999; Winter period: 02 November, 1999; 01 May, 2000; End Date: 15 May, 2000)

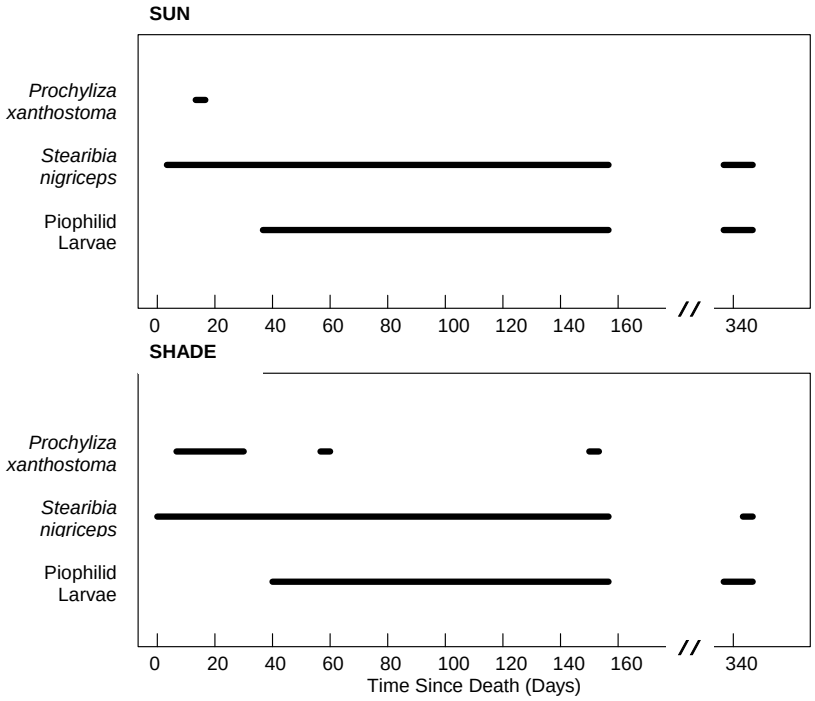


Figure 38. Time of arrival and duration of stay of the adult and larval Silphidae collected from pig carrion in sunny and shaded areas at Elm Creek. The slash marks denote the winter period (//). (Start date: 29 May, 1999; Winter period: 02 November, 1999 – 01 May, 2000; End Date: 15 May, 2000)

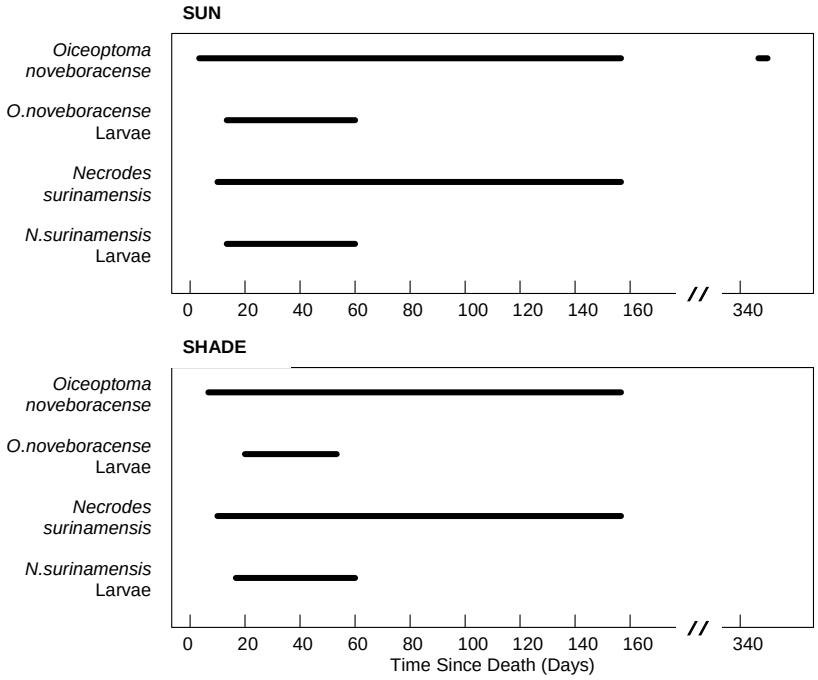


Figure 39. Time of arrival and duration of stay of the adult Staphylinidae collected from pig carrion in sunny and shaded areas at Elm Creek. The slash marks denote the winter period (//). (Start date: 29 May, 1999; Winter period: 02 November, 1999 – 01 May, 2000; End Date: 15 May, 2000)

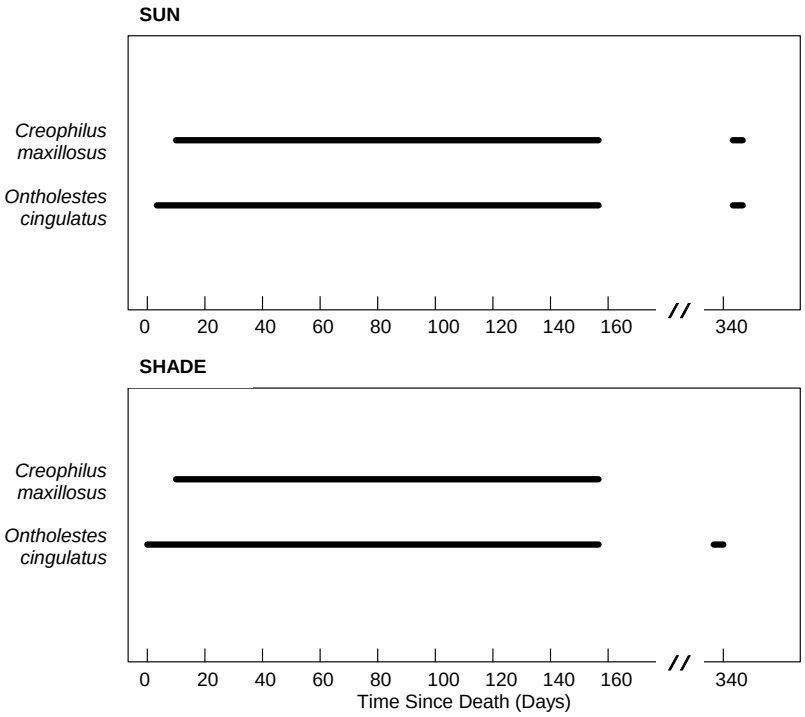


Figure 40. Time of arrival and duration of stay of the adult Cleridae collected from pig carrion in sunny and shaded areas at Elm Creek. The slash marks denote the winter period (//). (Start date: 29 May, 1999; Winter period: 02 November, 1999 – 01 May, 2000; End Date: 15 May, 2000)

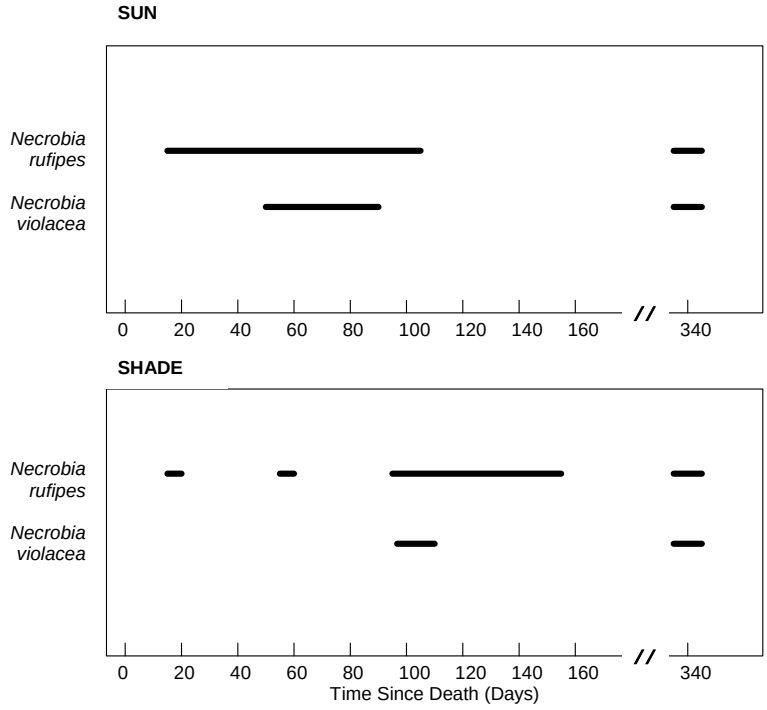


Figure 41. Time of arrival and duration of stay of the adult Nitidulidae and Dermestidae collected from pig carrion in sunny and shaded areas at Elm Creek. The slash marks denote the winter period (//). (Start date: 29 May, 1999; Winter period: 02 November, 1999 – 01 May, 2000; End Date: 15 May, 2000)

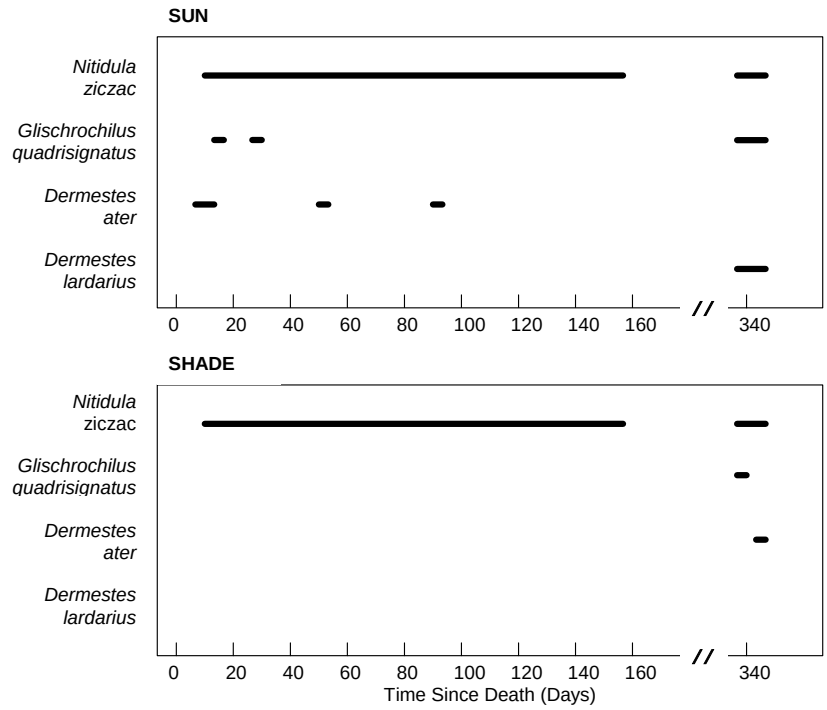


Figure 42. Time of arrival and duration of stay of the adult Trogidae and Geotrupidae collected from pig carrion in sunny and shaded areas at Elm Creek. The slash marks denote the winter period (//). (Start date: 29 May, 1999; Winter period: 02 November, 1999 – 01 May, 2000; End Date: 15 May, 2000)

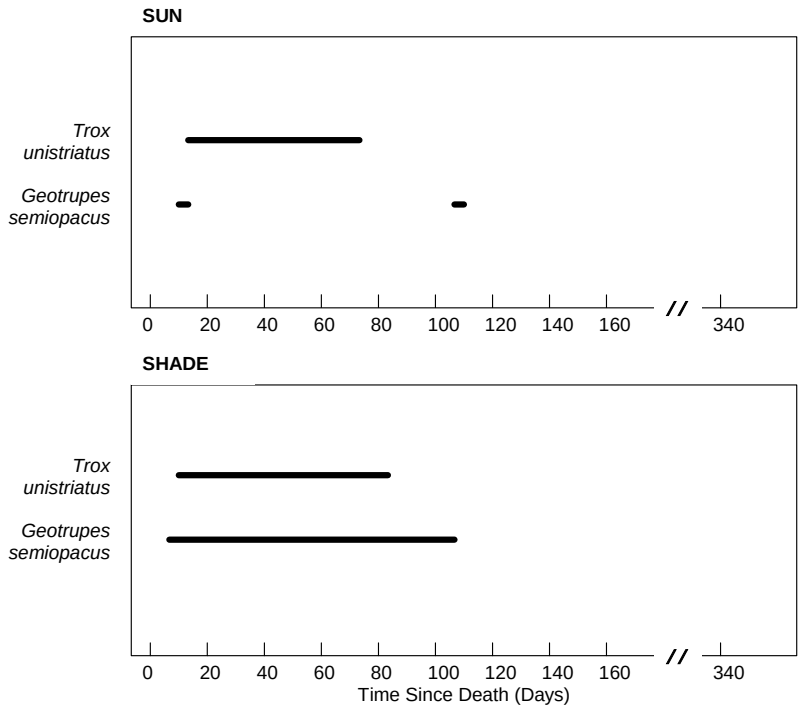


Figure 43. The duration of each stage of decomposition (in days) of pig carrion in sunny and shaded areas during the spring trial at Elm Creek. The slash marks denote the winter period (//).

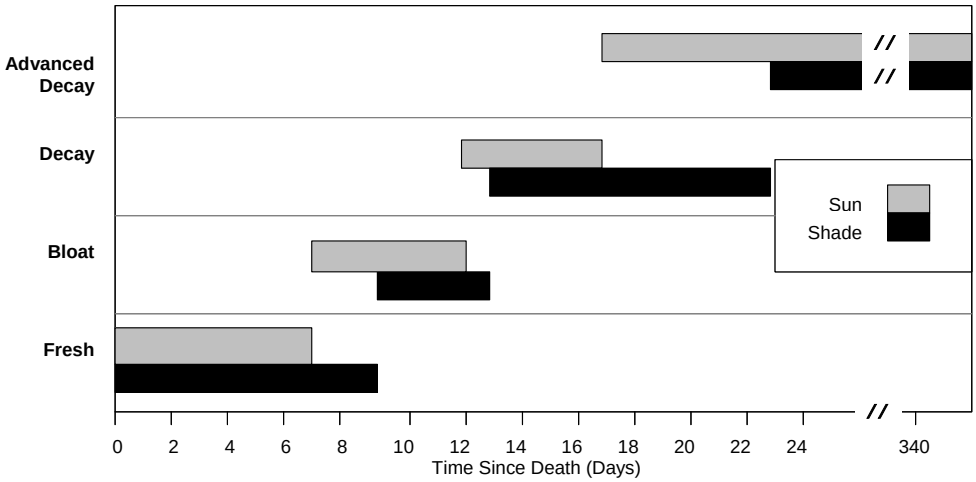


Figure 44. Photographs showing the colonization of calliphorids (A and B); putrefaction (C); and piophilid larvae (D) on pig carrion during the spring trial at Elm Creek.

A.

B.

C.

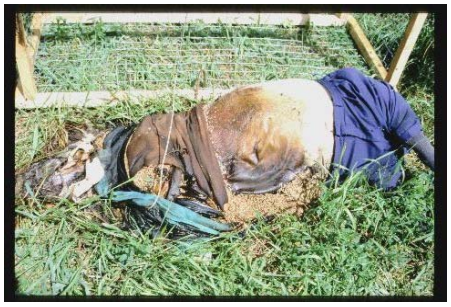
D.

Figure 45. A series of photographs illustrating the stages of decomposition of pig carrion during the spring trial at Elm Creek

A. Fresh

B. Bloat

C. Decay



D. Decay

E. Advanced Decay

F. Dry Remains

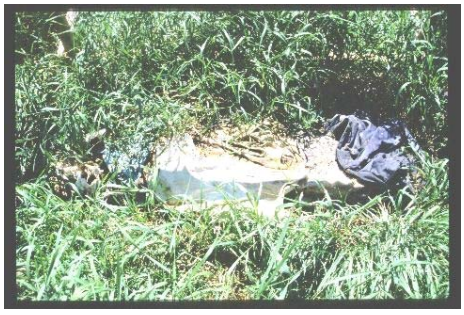


Figure 46. The biomass loss of pig carrion over time measured in kilograms in sunny and shaded areas at Elm Creek (n=1).

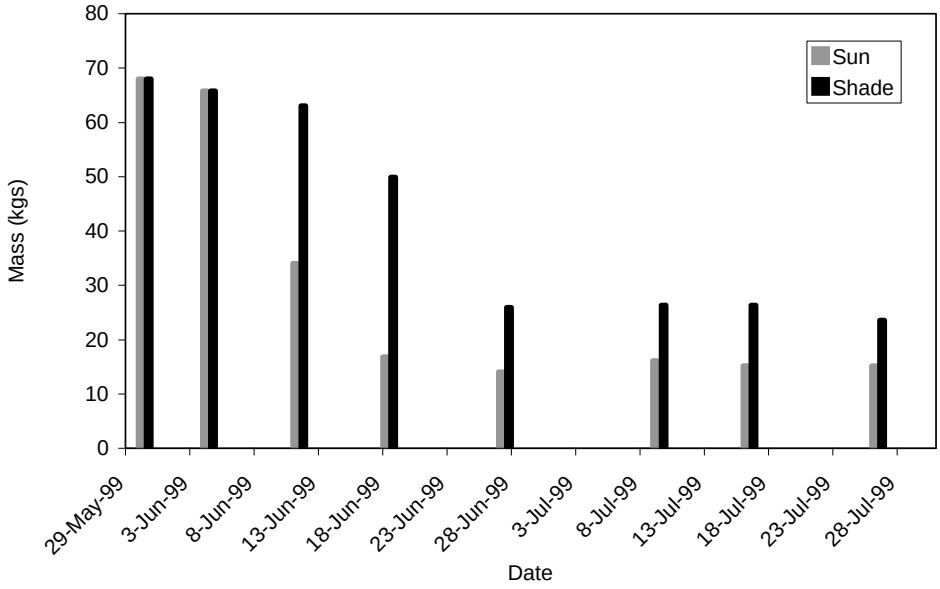


Figure 47. Average daily ambient air temperature in the sunny and shaded area during the spring trial at Elm Creek.

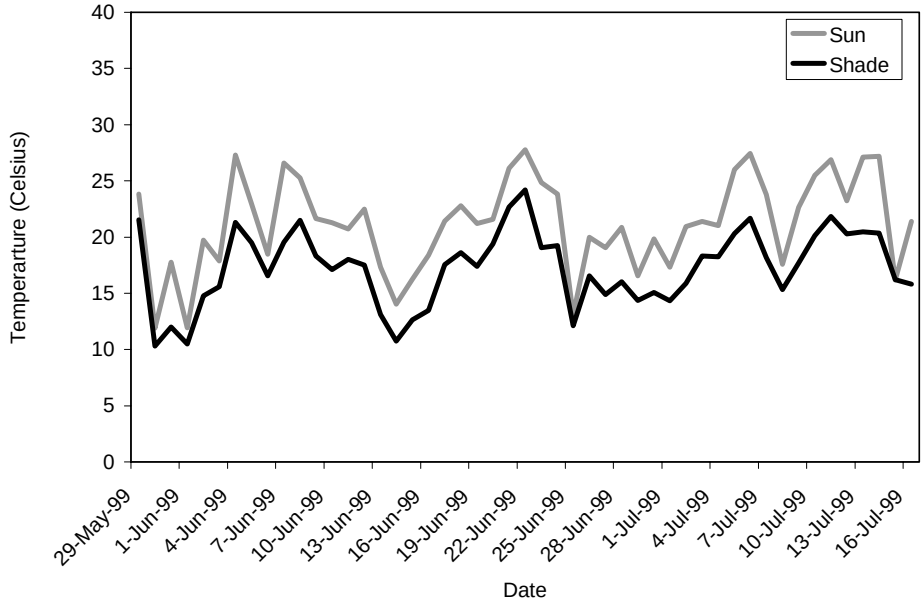


Table 1. Summary of the schedules related to each of the three trials conducted for the collection of necrophagous insects associated with pig carrion in sunny and shaded locations in Manitoba.

	Glenlea Research Station (GRS)	Sandilands Provincial Forest (SPF)	Elm Creek (EC)
Season	Summer	Fall	Spring
Day 0	30 June, 1998	29 August, 1998	29 May, 1999
End Date	01 September, 1999	31 August, 1999	15 May, 2000
Duration	426 days	367 days	347 days
Number of Pig Carcasses	6	8	8
Number of Pig Carcasses Sampled	4	4	4

Table 2. Mean numbers of maggots (±SE) collected per pitfall trap (n=4) associated with sun (pig carcasses B and D) and shade (pig carcasses A and C) exposed pig carrion within one-week time periods at Glenlea Research Station, Sandilands Provincial Forest and Elm Creek. (n.a. = Not available)

	Glenlea Research Station Summer		Sandilands Provincial Forest Fall		Elm Creek Spring	
Week	**Sun**	**Shade**	**Sun**	**Shade**	**Sun**	**Shade**
1	0 0	0 0	0 0	0 0	0.25 ± 0.25 0	0 0
2	950 ± 850 433 ± 258	1001 ± 470 2009 ± 734	2575 ± 418 4965 ± 907	4612 ± 1793 4168 ± 957	3 ± 2 35 ± 14	7 ± 3 24 ± 9
3	1471 ± 848 94 ± 53	7875 ± 2177 6861 ± 2486	n.a.	n.a.	n.a.	n.a.
4	0 0.25 ± 0.25	3 ± 2.5 0	3 ± 0.50 1 ± 0.60	18 ± 5 50 ± 10	16 ± 8 20 ± 3	n.a. 31 ± 24
5	0 0	0 0	1 ± 0.70 1 ± 0.50	37 ± 16 877 ± 366	1 ± 0.95 2 ± 1	3 ± 0.75 2 ± 0.30
			End of Sample Period			
6	0 0	0 0	-- --	-- --	0 0	0.25 ± 0.25 0.25 ± 0.25

Appendix 1. Presence and absence of the arthropod taxa collected from pig carcasses at Glenlea Research Station (GRS), Sandilands Provincial Forest (SPF) and Elm Creek (EC) in sunny and shaded areas. (+ =present; – =absent; × =not sorted from samples; ◘ =carrion feeders and/or breeders; † =new Manitoba record; ● =both larval and adult forms present).

	GRS (Summer)		SPF (Fall)		EC (Spring)	
	Sun	**Shade**	**Sun**	**Shade**	**Sun**	**Shade**
Class Arachnida						
O. Araneae	+	+	+	+	+	+
O. Opiliones	+	+	+	+	+	+
O. Acarina						
Mites	+	+	+	+	+	+
Ticks	+	+	+	+	+	+
O. Pseudoscorpiones	+	+	+	+	+	+
Class Diplopoda	+	+	+	+	+	+
Class Chilopoda	+	+	+	+	+	+
Class Hexapoda						
O. Orthoptera ●	+	+	+	+	+	+
O. Hemiptera ●	+	+	+	+	+	–
O. Homoptera ●	+	+	+	+	+	+
O. Neuroptera ●	+	+	+	+	+	–
O. Coleoptera Suborder Adephaga						
F. Carabidae ●	+	+	+	+	+	+
Agonum spp.	×	+	×	×	+	+
Agonum cupreum Dejean	×	×	×	×	+	+
Agonum placidum (Say)	×	×	×	×	+	+
Agonum retractum LeConte	×	×	×	×	+	+
Amara obesa (Say)	×	×	×	×	+	+
Anisodactylus verticalis (LeConte)	×	×	×	×	–	+
Bembidion spp.	×	×	×	×	–	+
Bembidion canadianum Casey	×	×	×	×	+	–
Bembidion quadrimaculatum Say	×	×	×	×	+	–
Chlaenius spp.	–	+	×	×	+	–
Dicaelus sculptilis Say	×	×	×	×	–	+
Diplocheila striatopunctatus (LeConte)	×	×	×	×	+	–
Harpalus spp.	×	×	×	×	+	–
Harpalus pensylvanicus (DeGeer)	×	×	×	×	+	+
Oxypselaphus pusillus (LeConte)	×	×	×	×	+	+
Platynus decentis (Say)	–	+	×	×	+	+
Poecilus lucublanda (Say)	+	–	×	×	+	–
Pterostichus spp.	×	×	×	×	+	–
Pterostichus melanarius (Illinger)	–	+	×	×	+	+

	GRS (Summer)		SPF (Fall)		EC (Spring)	
	Sun	Shade	Sun	Shade	Sun	Shade
Pterostichus pensylvanicus LeConte	×	×	×	×	+	+
Syntomus americanus (Dejean)	×	×	×	×	+	–
Synuchus impunctatus (Say)	×	×	×	×	+	+
Suborder Polyphaga						
F. Ptiliidae	–	–	–	–	+	+
F. Leiodidae	–	+	×	×	–	+
F. Silphidae ◘ ●	+	+	+	+	+	+
Heterosilpha ramosa (Say) ◘	–	–	+	–	+	–
Necrodes surinamensis (Fabricius) ◘ ●	+	+	+	+	+	+
Necrophila americana (Linnaeus) ◘	–	–	–	+	–	+
Nicrophorus defodiens Mannerheim◘	–	–	–	+	–	+
Nicrophorus hybridus Hatch and Angell◘	–	–	–	+	+	+
Nicrophorus obscurus Kirby◘	–	–	–	–	+	+
Nicrophorus orbicollis Say ◘	–	–	–	–	+	+
Nicrophorus pustulatus Hersch◘	–	–	–	–	+	+
Nicrophorus sayi Laporte◘	–	–	–	+	–	+
Nicrophorus tomentosus Weber ◘	–	–	–	–	+	+
Oiceoptoma noveboracensis (Forster) ◘	+	+	+	+	+	+
Thanatophilus lapponica (Herbst) ◘	+	+	–	–	+	–
F. Staphylinidae ◘ ●	+	+	+	+	+	+
Creophilus maxillosus (Linnaeus) ◘	+	+	+	+	+	+
Ontholestes cingulatus (Gravenhorst) ◘	+	+	+	+	+	+
Philonthus cyanipennis (Fabricius)	–	–	–	+	–	+
Staphylinus badipes LaConte	+	+	+	–	+	+
F. Hydrophilidae	+	+	+	+	+	+
Cercyon spp.	–	–	–	–	+	–
Sphaeridium spp.	–	–	–	–	+	–
F. Histeridae ◘	+	+	+	+	+	+
Acritus nigricornis (Hoffman)†	+	–	–	–	–	–
Atholus americanus (Paykull)	×	×	×	×	+	–
Atholus falli Bickhardt	×	×	×	×	+	–
Carcinops pumilio (Erichson)	+	+	+	+	+	+
Euspilotus assimilis (Paykull)	×	×	×	×	+	–
Geomysaprinus cheyennensis (Casey)	×	×	×	×	+	–
Hister abbreviatus Fabricius	×	×	×	×	+	–
Hister furtivus LeConte	×	×	×	×	+	+

	GRS (Summer)		SPF (Fall)		EC (Spring)	
	Sun	Shade	Sun	Shade	Sun	Shade
Margarinotus brunneus (Fabricius) †	×	×	×	×	+	–
Margarinotus harrisii (Kirby)	×	×	×	×	–	–
Margarinotus hudsonicus (Casey)	×	×	×	×	+	+
Margarinotus immunis (Erichson)	×	×	×	×	+	+
Margarinotus lecontei *Wenzel*	×	×	×	×	+	+
Saprinus sp.	×	×	×	×	–	–
Saprinus lugens Erichson	×	×	×	×	+	+
Saprinus oregonensis LeConte	×	×	×	×	+	+
F. Eucinetidae	×	×	×	×	+	+
F. Lucanidae	×	×	×	×	+	–
F. Scarabaeidae ◘	+	+	+	+	+	+
Aphodius spp.	+	–	×	×	+	+
Dichelonyx spp.	–	–	×	×	+	–
Onthophagus spp.	+	–	×	×	+	–
Onthophagus hecate (Panzer)	+	–	×	×	+	+
Onthophagus nuchicornis (Linnaeus)	–	+	×	×	+	+
F. Geotrupidae ◘	–	–	+	+	+	+
*Bolboceras falli (*Wallis)	–	–	–	–	–	+
Geotrupes semiopacus Jekel	–	–	+	+	+	+
F. Trogidae ◘	+	+	+	+	+	+
Trox unistriatus Beauvois	+	+	+	+	+	+
F. Elateridae	–	–	–	–	+	+
F. Dermestidae ◘ ●	+	+	+	+	+	+
Dermestes ater DeGeer	–	–	+	+	–	+
Dermestes fasciatus LeConte◘	+	–	–	–	+	–
Dermestes frischi Kugelann◘†	+	–	–	–	+	–
Dermestes lardarius Linnaeus ◘	+	+	+	–	+	+
Dermestes signatus LeConte◘	–	+	–	–	–	–
F. Cleridae ◘ ●	+	+	+	+	+	+
Necrobia rufipes (DeGeer)◘ †	+	+	+	–	+	+
Necrobia violacea (Linnaeus)◘	+	+	+	+	+	+
F. Nitidulidae ◘ ●	+	+	+	+	+	+
Glischrochilus quadrisignatus (Say)	+	+	–	–	+	+
Nitidula bipunctata (Linnaeus)◘	+	–	–	–	–	–
Nitidula nigra Schaeffer ◘	+	–	+	+	–	–
Nitidula ziczac Say ◘	+	+	+	+	+	+
F. Rhizophagidae	×	×	×	×	–	–

	GRS (Summer)		SPF (Fall)		EC (Spring)	
	Sun	**Shade**	**Sun**	**Shade**	**Sun**	**Shade**
F. Cucujidae	×	×	×	×	+	–
F. Cryptophagidae	×	×	×	×	+	+
F. Phalacridae	×	×	×	×	+	+
F. Coccinellidae	×	×	×	×	+	–
F. Lathridiidae	×	×	×	×	+	+
F. Mycetophagidae	×	×	×	×	+	–
F. Tenebrionidae	×	×	×	×	–	+
F. Meloidae	×	×	×	×	+	–
F. Anthicidae	×	×	×	×	+	+
F. Chrysomelidae	×	×	×	×	+	+
F. Curculionidae	×	×	×	×	+	+
O. Mecoptera	×	×	×	×	–	+
O. Diptera Suborder Nematocera						
F. Bibionidae	×	×	×	×	+	+
F. Mycetophilidae	×	×	×	×	+	–
F. Cecidomyiidae	×	×	×	×	+	+
F. Sciaridae	+	+	×	×	+	+
F. Scatopsidae	–	–	–	–	+	+
F. Culicidae	+	–	+	+	–	+
F. Ceratopogonidae ●	+	–	×	×	+	+
F. Chironomidae ●	×	×	×	×	+	–
Suborder Brachycera						
F. Rhagionidae	–	–	–	–	–	+
F. Stratiomyidae	–	–	–	–	+	+
F. Therevidae	–	+	–	–	+	-
F. Empididae	+	+	–	–	+	+
F. Dolichopodidae	+	+	–	–	+	+
F. Syrphidae ●	+	+	–	–	–	–
Section Acalyptratae						
F. Micropezidae	–	–	–	–	–	+
F. Otitidae	+	–	–	–	–	–
Physiphora spp.	+	–	–	–	–	–
F. Piophilidae ◘ ●	+	+	+	+	+	+
Boreopiophila tormentosa Frey ◘	+	–	–	–	–	–
Prochyliza xanthostoma Walker◘	+	+	+	+	+	+
Stearibia nigriceps (Meigen)◘	+	+	+	+	+	+
F. Sciomyzidae	+	–	×	×	×	×
F. Sepsidae	+	+	+	+	+	+
F. Lauxaniidae	–	–	×	×	–	+
F. Heleomyzidae	–	–	×	×	+	+
F. Sphaeroceridae	+	+	+	+	+	+
Coproica spp.	×	×	×	×	+	+
Ischiolepta spp.	×	×	×	×	+	+
Leptocera spp.	×	×	×	×	+	+
Sphaerocera curvipes Latrielle	+	+	+	+	+	+

	GRS (Summer)		SPF (Fall)		EC (Spring)	
	Sun	**Shade**	**Sun**	**Shade**	**Sun**	**Shade**
F. Drosophilidae	+	+	+	+	+	–
F. Chloropidae	+	+	×	×	+	+
Section Calyptratae						
F. Scathophagidae ●	–	+	×	×	+	+
F. Anthomyiidae	+	+	×	×	+	+
F. Muscidae ◘ ●	+	+	+	+	+	+
Fannia sp.	+	+	+	+	+	+
Musca domestica Linnaeus	+	+	×	×	×	×
Muscina sp.	+	+	×	×	×	×
Stomoxys calcitrans (Linnaeus)	–	+	×	×	×	×
F. Calliphoridae ◘ ●	+	+	+	+	+	+
Calliphora terraenovae Macquart ◘	+	–	–	–	–	+
Calliphora vicina Robineau-Desvoidy ◘	+	–	–	–	–	+
Calliphora vomitoria (Linnaeus) ◘	–	–	+	+	–	+
Cynomya cadaverina (Robineau-Desvoidy) ◘	–	–	–	–	+	+
Lucilia illustris (Meigen)◘	+	+	+	+	+	+
Phaenicia sericata (Meigen)◘ ●	+	–	–	–	–	–
Phormia regina (Meigen)◘ ●	+	+	+	+	+	+
Protophormia terraenovae (Robineau-Desvoidy) ◘	+	+	–	+	+	+
F. Sarcophagidae ◘ ●	+	+	+	+	+	+
O. Lepidoptera ●	+	+	+	+	+	+
O. Hymenoptera	+	+	+	+	+	+
F. Eulophidae	–	+	–	–	–	–
F. Formicidae	+	+	+	+	+	+
F. Sphecidae	+	+	+	+	+	+
F. Vespidae	+	+	+	+	–	–
Dolichovespula sp.	–	–	+	+	–	–
Vespula spp.	+	+	+	+	–	–