INSECT SUCCESSION ON CARRION IN THREE BIOGEOCLIMATIC ZONES OF BRITISH COLUMBIA

by

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ABSTRACT

I examined habitat, season, and geographic location as factors that affect the development, species and sequence of insects associated with pig carcasses in British Columbia between 1994 and 1996. Development rates of immature Calliphoridae (blow flies) and insect succession on pig carcasses varied with habitat, season and biogeoclimatic zone. High temperatures, presence of clothing and scavenging contributed to fast decomposition, whereas cold temperatures, lack of clothing and lack of moisture contributed to slow decomposition rates. Blow fly species were not exclusively associated with a particular habitat or season. However, *Calliphora vomitoria*, *Lucilia illustris*, and *Protophormia terraenovae* possibly had biogeoclimatic preferences. Colonization by flies in the families Piophilidae and Fanniidae and beetles in the family Dermestidae occurred earlier than that reported in other regions. Colonization by piophilids and fanniids was delayed or absent on scavenged, or desiccated carcasses and on carcasses subjected to cold temperatures. Few habitat or seasonal preferences were distinguishable among beetles in the families Cleridae and Dermestidae. However, low moisture associated with particular seasons and zones was related to the presence of insects in these families. Clothing increased insect diversity on carcasses, whereas scavenging by vertebrates reduced insect diversity. Decomposition rates of and insect succession on black bear and cougar carcasses were broadly similar to those for clothed pigs. The species of insects and their development rates on pig and wildlife carcasses provide forensic standards that can be used to determine time since death of humans and wildlife.

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1. INTRODUCTION

1.1 Overview

Insects play a fundamental ecological role in the decomposition of organic material. Often the first witnesses to a death, they arrive in a predictable sequence (Smith 1986) that is influenced by biological, chemical and physical changes that occur in carrion as it decomposes. When the sequence of insects colonizing carrion is known, an analysis of the insect fauna can be used to answer forensic questions.

One of the most pressing forensic tasks is to determine the time of death. Recent research has expanded on the use of insect succession as a means of establishing the time of death. Multiple stages of decomposition influence identifiable and predictable successional stages of insect diversity and activity (Goff 1993). These successional stages are influenced by factors such as habitat, season and location. Research has established some data bases for different conditions that allow insect data to be used with confidence in forensic investigations. However, previous research may have limited application because of a lack of experimental rigor. Past experimental shortcomings include: incomplete identification of insects (Rodriguez & Bass 1983; Chapman & Sankey 1955); deployment of frozen carcasses (Goddard & Lago 1985; Johnson 1975; Payne 1965); unknown time of death of carcasses (Smith 1975; Burger 1965); lack of replication (Schroeder *et al.* 1995; Shean *et al.* 1993; Hewadikaram & Goff 1991; Jiron & Cartin 1981; Johnson 1975; Smith 1975; Easton 1966; Burger 1965; Chapman & Sankey 1955); lack of controls (Schroeder *et al.* 1995; Shean *et al.* 1993; Hewadikaram & Goff 1991; Jiron & Cartin 1981; Johnson 1975; Smith 1975; Easton 1966; Burger 1965; Chapman & Sankey 1955); and failure to use suitable animal models (Kneidel 1984).

To be of scientific value and transferable to forensic purposes, research design must be precise, must include replication and should use realistic animal models. This is true in all experiments, but is especially true when the application of such research may result in the conviction or exoneration of a person accused of murder or poaching.

1.2 Background

The use of entomology in criminal investigations began as early as the 13th century (McKnight 1981). However, forensic entomology did not develop as a means to determine time of death until the late 19th century. Pioneers in this field (Motter 1898; Brouardel 1897; Johnston &

Villeneuve 1897; Mégnin 1894; Yovanovitch 1888; Bergeret 1855) recognized the value of insect patterns on exposed human cadavers, a realization that has guided subsequent research on human remains (Goff 1991; Galloway *et al.* 1989; Rodriguez & Bass 1983) and non-human carrion (Anderson & VanLaerhoven 1996; Goff 1993; Schoenly *et al.* 1991; Jiron & Cartin 1981; Denno & Cothran 1976; Smith 1975; Payne *et al.* 1968; Burger 1965; Payne 1965; Chapman & Sankey 1955; Morley 1907).

In Canada, the science of forensic entomology is approaching the 100th anniversary of Johnston and Villeneuve's (1897) pioneering comparative study of forensic entomology. It addressed the influence of biogeoclimatic differences on insect succession on humans in two locations: Paris, France and Montreal, Quebec. Among the differences observed were "successions of insect forms occurred in a shorter time on exposed bodies (in Quebec)" and species diversity differed at the two locations. As a result, Johnston and Villeneuve (1897) urged that "observations and experiments upon exposed human bodies should be made in the particular locality before the present entomological data can be directly applied to legal medicine".

Almost a century later, Skinner *et al.* (1988) published the first Canadian paper on the use of insects to determine time of death of a homicide victim. Unfortunately, because of a lack of local research, the conclusions were based on data from other geographic locations primarily outside of North America. Controlled, regional, carrion research is considered to be a prerequisite to the application of entomology to forensics (Tantawi *et al.* 1996; Anderson 1995; Schoenly *et al.* 1991; Smith 1986).

McKeown (1991) linked the paucity of research and case work in Canada to the relatively small number of homicides, and predicted that the need for this information will increase as the Canadian population increases. Overlooked to date is the application of forensic entomology to wildlife poaching investigations. However, applications are constrained by a lack of reliable baseline data and insufficient awareness of the usefulness of entomological methods as an investigative tool. There is a need to establish databases of insect succession for use in both human and non-human subjects so that forensic entomology can be used with confidence in Canada.

The first Canadian experiment that examined insect activity on carrion was conducted in 1992 in the Lower Fraser Valley of British Columbia (B.C.) by Anderson & VanLaerhoven (1996). This research documented insect arrival times and established their sequence of succession on unclothed pig carcasses located in one habitat, during one season, and one

geographic location. One conclusion was that insect succession in B.C. differed from that in areas with a similar climate in Europe. The research reported herein builds on the recommendation by Anderson & VanLaerhoven (1996) that further research be conducted to understand these differences.

1.3 Rationale

From 1988 to 1994, 83.3 % of human death investigations using forensic entomology in B.C. (Anderson 1995) were located in the Coastal Western Hemlock (CWH) biogeoclimatic zone (Meidinger & Pojar 1991). Thus, there was interest and need to develop standards for this zone. The Interior Douglas-fir (IDF) and Sub-boreal Spruce (SBS) zones reflected only 2.4 % and 7.1 % of investigations using insect evidence (Anderson 1995). However, these percentages are probably artificially low because most coroners, and law enforcement officers located in these zones were unaware of forensic entomology as an investigative tool (Lazzarotto 1995; Slavens 1995; Tait 1995). The development of insect standards as well as awareness and training in forensic entomological procedures will benefit enforcement agencies in these zones and will increase numbers of cases that use insects.

Experiments were needed to examine the decomposition rate of carcasses and insect succession in two main environments: sun and shade. Of the few international decomposition studies that take habitat into consideration, results have shown differences in times of arrival and species composition of insects (Shean *et al.* 1993; Lane 1975; Reed 1958; Chapman & Sankey 1955). Examination of carcasses in both sunny and shady habitats allows for the extrapolation of data to human and wildlife death investigations located in either habitat.

Seasonal variation has been documented as a factor that influences insect activity (Smith 1986; Goddard & Lago 1985; Rodriguez & Bass 1983; Johnson 1975; Reed 1958). Decomposition experiments in the CWH zone must examine insect activity in the spring, summer and fall. The weather in this zone is mild (Meidinger & Pojar 1991) and hence insect activity is expected in all three seasons. Experiments in both the IDF and SBS zones were required only in spring and summer because the onset of cold temperatures in the fall restricts insect activity.

Seventy-nine percent of all entomological cases analyzed from 1988-1995 in British Columbia involved bodies which were clothed or wrapped in cloth (Anderson 1996). Therefore, the inclusion of clothing in carrion experiments provides a realistic scenario for human death investigations.

Ideally, data for use in human death investigations should be developed using human models. However, because of moral, ethical, practical, and logistical reasons, few researchers have performed successional ecological research on human cadavers (Mann *et al.* 1990; Galloway *et al.* 1989; Rodriguez & Bass 1983; Watkins 1983). As a result, most researchers have chosen animal models to develop baseline data for use in human death investigations (Anderson & VanLaerhoven 1996; Shean *et al.* 1993; Goff 1991a; Hewadikaram & Goff 1991; Goddard & Lago 1985; Kneidel 1984; Jiron & Cartin 1981; Denno & Cothran 1976; Johnson 1975; Payne 1965; Reed 1958; Chapman & Sankey 1955; Howden 1950). Despite reservations by researchers when using non-human carrion data to estimate time of death of humans (Schoenly *et al.* 1991; Mann *et al.* 1990; Johnston & Villeneuve 1897), data from decompositional studies using non-human subjects have been applied with success in homicide investigations (Anderson & VanLaerhoven 1996; Goff 1993).

Domestic pig carcasses, *Sus scrofa* L., have been recognized as the most acceptable animal model for human decomposition (Goff 1993; Catts & Goff 1992). Freshly killed pigs should be used for carrion experiments because frozen-thawed carcasses may not provide an accurate picture of decomposition sequences and timing (Micozzi 1991).

Wildlife carcasses are an unpredictable source for carrion ecological studies. The killing of wildlife for research purposes is rarely permitted and highly controversial and may explain why so few researchers have used wild animals as research subjects (Braack 1981; Coe 1978; Smith 1975; Nuorteva & Hasanen 1972; Easton 1966). The focus of these studies has been diverse and none was conducted specifically to generate baseline insect data for wildlife death investigations.

1.4 Research Objectives

My research examined and compared carrion ecology in different habitats, seasons and geographic regions of British Columbia. It addressed two main applications: human death investigations using pig carcasses as human models; and wildlife death investigations using bear and cougar carcasses. The objectives were to:

1. record developmental rates of Calliphoridae in a natural setting and to identify and compare patterns of insect succession;

2. determine the sequence of insect succession on pig carcasses in three biogeoclimatic zones (CWH, IDF, and SBS) of B.C., two habitats (sun and shade), and three seasons (spring, summer and fall);

3. determine whether patterns of insect succession on wildlife carcasses are predictable; and

4. to relate these data to human and wildlife death investigations.

2. METHODS AND MATERIALS

2.1 Research Locations

Research locations in Maple Ridge, 150 Mile House, and Gavin Lake were chosen within three biogeoclimatic zones (CWH, IDF and SBS respectively) in British Columbia (Meidinger & Pojar 1991) (Figures 1-3). An open, exposed, sunny habitat (sun) and a shaded woodland habitat (shade) were selected in each zone. Experiments in the CWH zone were conducted during spring, summer and fall of 1994. In both the IDF and SBS zones, experiments took place during spring and summer 1995.

The research locations were within Research Forest Blocks owned by the University of British Columbia. These limited public access, minimized potential tampering with the experiments, and were in rural areas to allow for natural insect associations with carcasses and to avoid possible bias from urbanization.

Because decomposing carcasses in remote research locations can attract animals such as grizzly and black bears, cougars, and wolverines, warning letters were sent to all local residents and ranchers, caution signs were posted at all carcass sites and carcasses were placed close to service roads to provide quick escape for researchers. A chemical repellent (Bear Phaser®, Arvis Corp.), a loud sound device (*i.e.* air horn), and a cellular/radio phone were carried at all times during field work.

Figure 1. **Distribution of the Coastal Western Hemlock (CWH) biogeoclimatic zone. From Meidinger & Pojar (1991).**

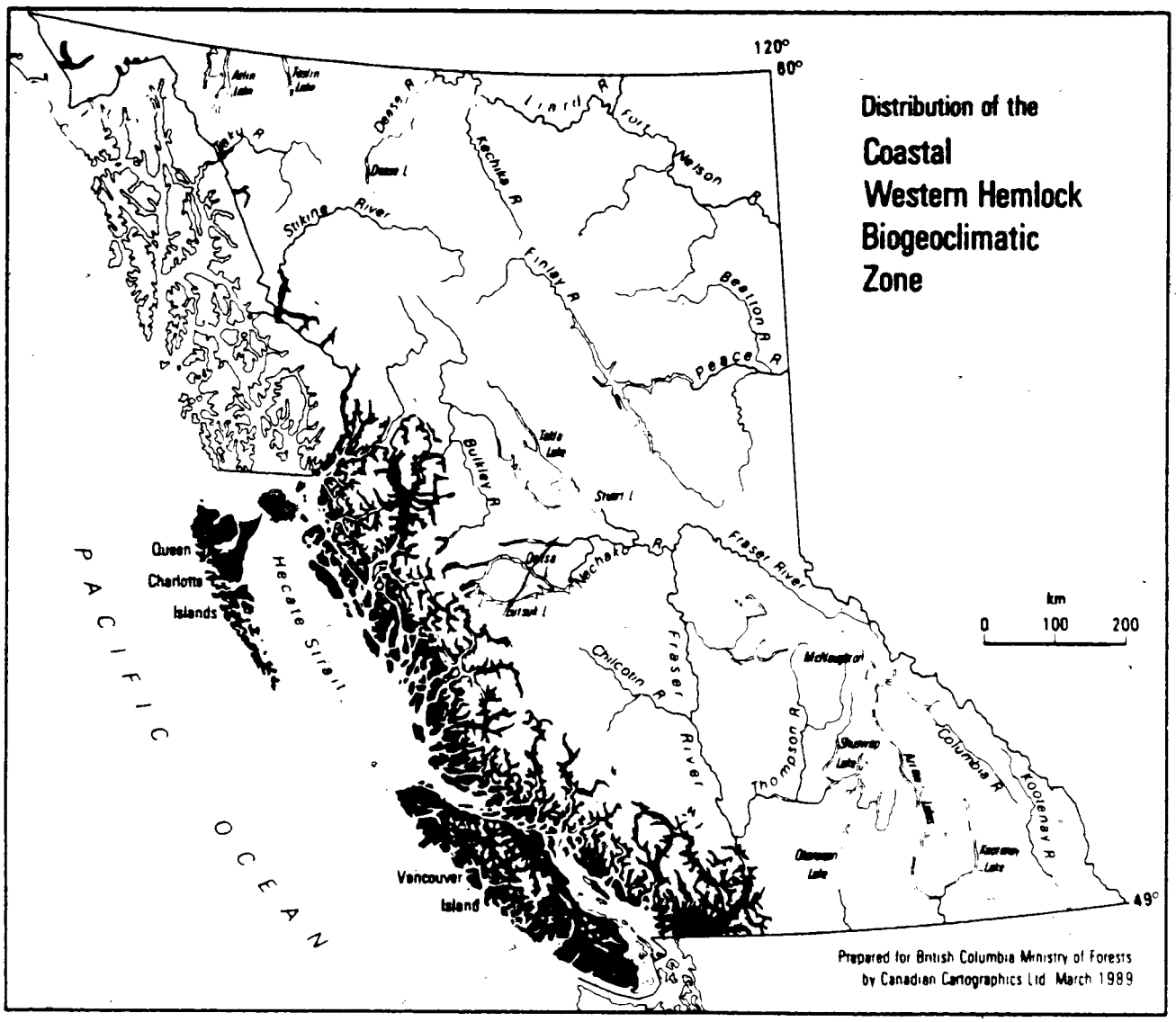

Distribution of the
Coastal
Western Hemlock
Biogeoclimatic
Zone
120°
60°
49°
Liard R
Fort Nelson R
Kechika R
Finlay R
Beatton R
Peace R
Stikine River
Dease R
Dease L
Turnagain R
Kwadacha R
Bulkley R
Stuart L
Fraser River
Chilcotin R
Fraser River
Thompson R
Columbia R
Kootenay R
Queen Charlotte Islands
Hecate Strait
Vancouver Island
PACIFIC OCEAN
km
0 100 200
Prepared for British Columbia Ministry of Forests
by Canadian Cartographics Ltd March 1989

Figure 2. Distribution of the Interior Douglas-fir (IDF) biogeoclimatic zone. From Meidinger & Pojar (1991).

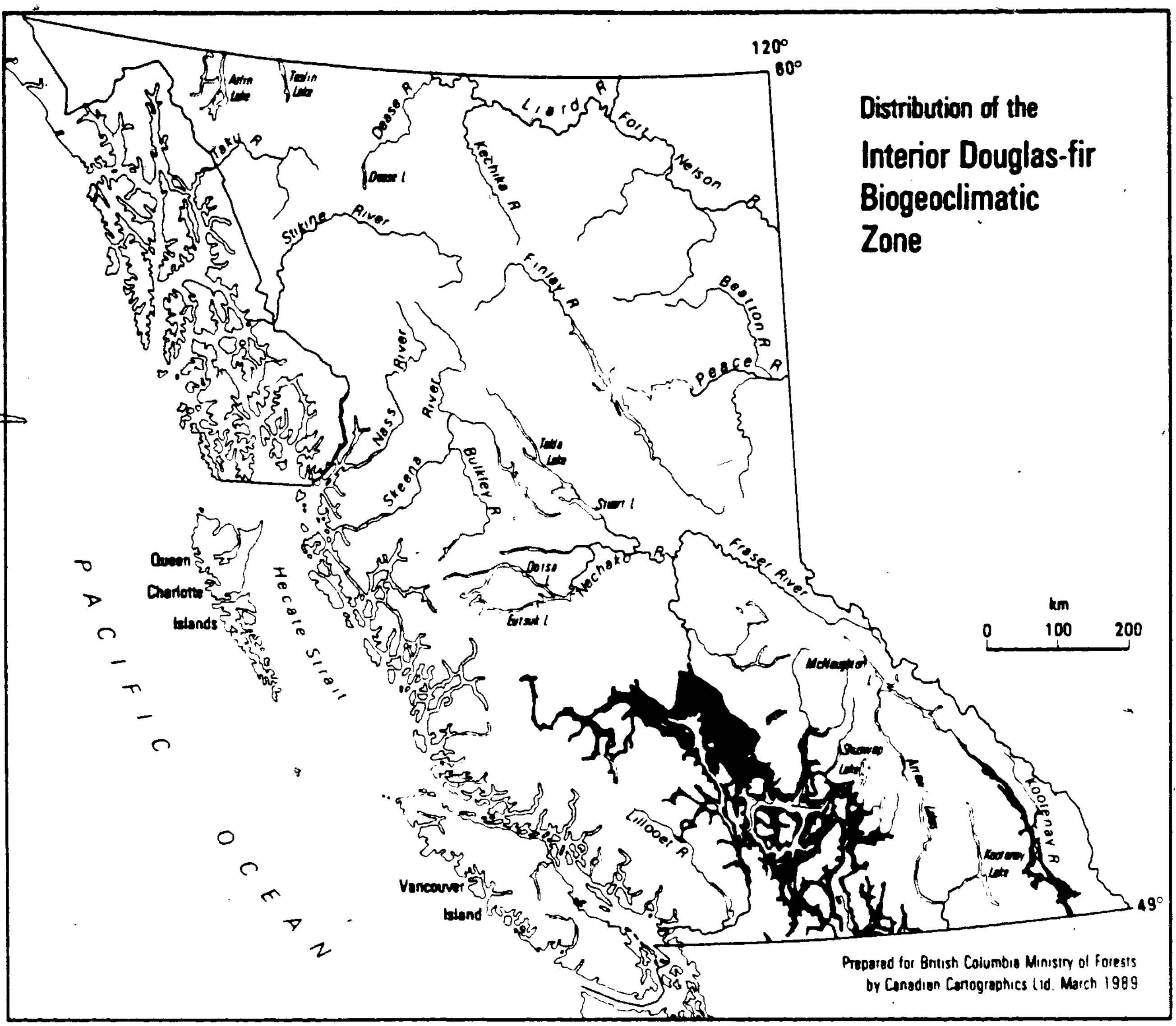
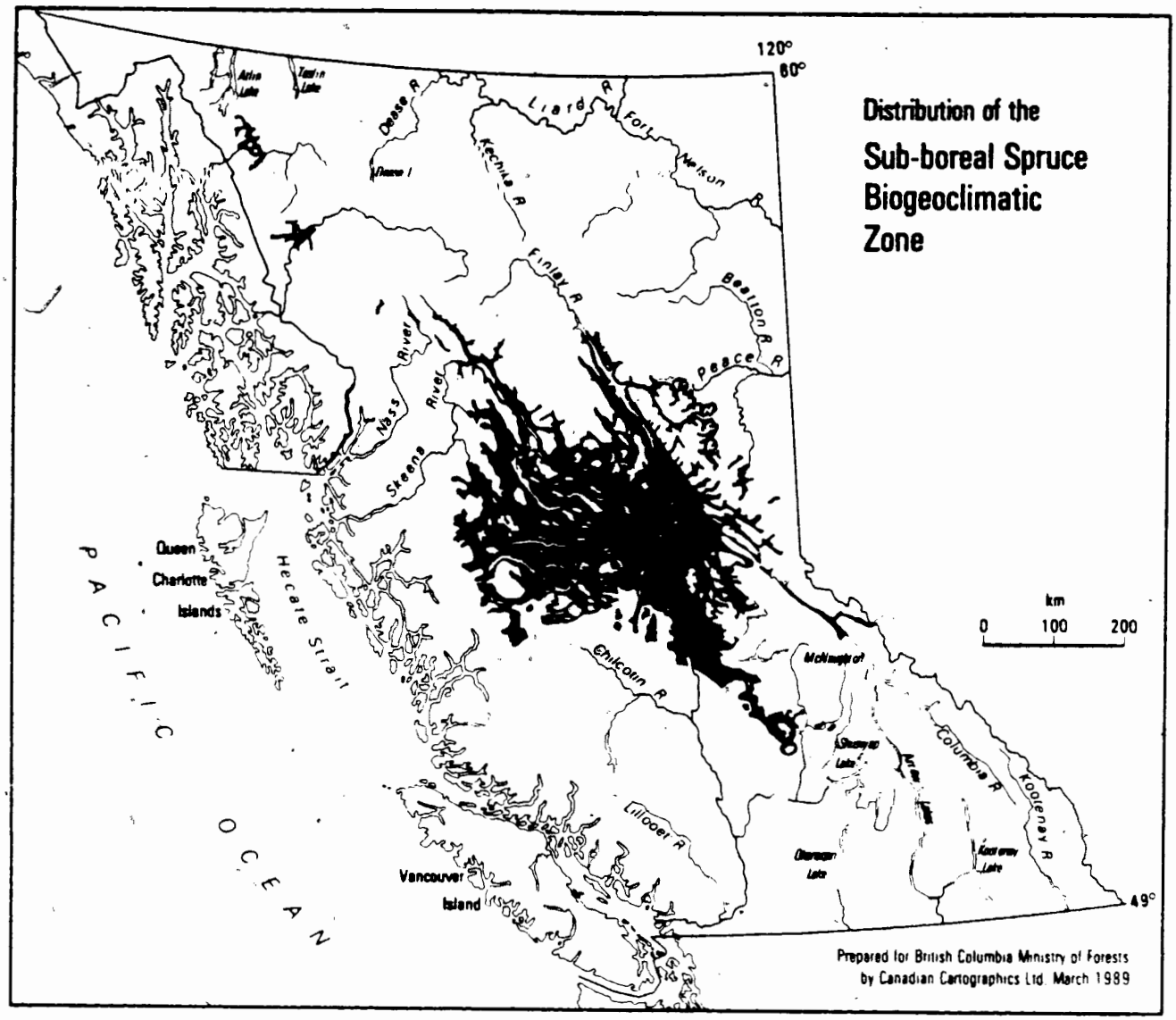

Distribution of the
Interior Douglas-fir
Biogeoclimatic
Zone
120°
60°
49°
km
0 100 200
Taku R
Stikine River
Dease R
Liard R
Fort Nelson R
Kechika R
Finlay R
Beatton R
Peace R
Nass River
Skeena River
Bulkley R
Nechako R
Fraser River
Lillooet R
Kootenay R
Queen Charlotte Islands
Hecate Strait
Vancouver Island
PACIFIC OCEAN
Prepared for British Columbia Ministry of Forests
by Canadian Cartographics Ltd. March 1989

Figure 3. Distribution of the Sub-Boreal Spruce (SBS) biogeoclimatic zone. From Meidinger & Pojar (1991).


Distribution of the
Sub-boreal Spruce
Biogeoclimatic
Zone
120°
60°
49°
Liard R
Fort Nelson R
Finlay R
Beatton R
Peace R
Nass River
Skeena River
Queen Charlotte Islands
Hecate Strait
PACIFIC OCEAN
Vancouver Island
Chilcotin R
Columbia R
Kootenay R
Lillooet R
km
0 100 200
Prepared for British Columbia Ministry of Forests
by Canadian Cartographics Ltd. March 1989

2.2 Experimental Design for Pigs

Seventy-two pig carcasses, freshly killed, weighing approximately 23 kg each were used (Table 1). Two undersized carcasses were rejected. All pigs were killed in an abattoir by a single shot to the head from a 15-cm pin gun. All carcasses were shot a second time with a .22 caliber bullet in the side of the chest. This bullet hole was used in control carcasses to insert a temperature probe. Freshly killed carcasses were transported within 4 h to the research locations. All carcasses were placed at least 50 m apart in cages designed to exclude large carnivores and to allow free access by insects, rain and sunlight. Although 100 m between carcasses is recommended (Schoenly *et al.* 1991), this was not practical nor feasible considering the available sites, and safety precautions required. Each cage was 105 cm long, 75 cm wide, and 45 cm high and was constructed with 1 cm^2 steel bars, spaced 4 cm apart (Photograph 1). Cage tops were hinged to open upwards, and were bolted closed with 0.8 by 3 cm bolts. All cages were secured to the ground with four 45-cm-long steel spikes. Each experimental carcass was placed in the cage on a wire mesh platform, which could be raised by a pulley system and weighed on a scale hanging from a steel tripod (Photograph 2).

Pitfall traps were used to collect both diurnal and nocturnal crawling insects associated with the carcasses as well as incidental insect species in the area. Each trap consisted of a 250 mL jar buried so that the lip was flush with the surface of the ground. Soapy water was placed in the bottom to trap insects. Initially at each cage, four pitfall traps were placed within 5 cm of each cage side. After no carcass or compass directional bias was found, only one trap was used. Control traps were placed approximately 20 m from the carcass site. Collections were made by pouring the contents of each jar through a labeled piece of cloth. Insects collected on the cloth were identified, recorded and preserved.

Temperature dataloggers (SmartReader 1®, Young Environmental Systems Inc.) were programmed to record ambient and internal carcass temperatures every 0.5 h.

2.3 Experimental Methods for Pigs

The experimental design was based on that used by Anderson and VanLaerhoven (1996). Each experiment used 10 carcasses: three experimental and two control carcasses located in each habitat, sun and shade.

The experimental carcasses were weighed during the fresh, bloat and decay stages of decomposition. Each carcass was photographed and examined for insect activity immediately

TABLE 1. Time of death and location of 72 pig carcasses, 1994-1995.

NUMBER OF CARCASSES	IDENTIFICATION NUMBERS	DATE OF DEATH	SEASON OF PLACEMENT	BIOGEOCLIMATIC ZONE	HABITAT
5	1-5	21-May-94	Spring	Coastal Western Hemlock	Sun
5	6-10	21-May-94	Spring	Coastal Western Hemlock	Shade
5	11-15	16-Jul-94	Summer	Coastal Western Hemlock	Sun
5	16-20	16-Jul-94	Summer	Coastal Western Hemlock	Shade
5	21-25	24-Sep-94	Fall	Coastal Western Hemlock	Sun
5	26-30	24-Sep-94	Fall	Coastal Western Hemlock	Shade
2	31-32	24-Sep-94	Fall	Coastal Western Hemlock	Sun
5	33-37	19-May-95	Spring	Interior Douglas-Fir	Shade
5	38-42	19-May-95	Spring	Interior Douglas-Fir	Sun
5	43-47	12-Jul-95	Summer	Interior Douglas-Fir	Shade
5	48-52	12-Jul-95	Summer	Interior Douglas-Fir	Sun
5	53-57	18-May-95	Spring	Sub-boreal Spruce	Sun
3	58-60	18-May-95	Spring	Sub-boreal Spruce	Shade
2	61,62	19-May-95	Spring	Sub-boreal Spruce	Shade
5	63-67	11-Jul-95	Summer	Sub-boreal Spruce	Sun
5	68-72	11-Jul-95	Summer	Sub-boreal Spruce	Shade

Carcasses 31-32 were clothed to monitor effects of clothing; they were examined, but not included in the successional analysis.

after placement, and then every second day for approximately four to six weeks. They were then sampled weekly until no further insects were observed. On each sampling day, colour photographs of each carcass were taken with a Nikon® F-601 AF, Quartz date, 35 mm camera, with a Tamron® AF 24-70 mm F/ 3.3-5.6 aspherical lens. The carcass was raised briefly and the insects beneath it were collected. Immature and adult insects associated with experimental carcasses and in pitfall traps were also collected on each sampling date.

All larval Calliphoridae and Sarcophagidae were examined under a binocular microscope to determine instar by numbers of spiracular slits (Smith 1986). Immature specimens were raised to adulthood on beef liver to confirm identification. Immature stages of insects belonging to other families were raised in the laboratory or preserved, depending on ease of identification. Maggot mass temperatures were recorded during bloat and decay stages using a hand-held thermometer (Photograph 3).

The control carcasses, together with their insect fauna, were observed, but not disturbed, except that the contents of their pitfall traps were collected regularly. Ambient and internal carcass temperatures were recorded for each control carcass. Internal temperatures were obtained by inserting a temperature probe approximately 8 to 10 cm into the bullet wound in the torso (Photograph 4). The temperature probe was connected to an automatic datalogger which could be downloaded into a computer (Photograph 5). Ambient and internal pig carcass temperatures during the bloat and decay stages were compared using linear regressions (Microsoft Excel®).

In the CWH zone during 1994, I used the experimental method described above for spring, summer, and fall experiments. In the fall, two additional carcasses, fully clothed, were deployed in preparation for observations 1995.

During spring and summer 1995, the experiments were repeated in the IDF and SBS zones. Three minor changes to the protocol were made. The distance between cages was reduced to 45 m, pigs were clothed and clothing was also examined for insect activity (Photograph 6), and sampling was done every 3-4 days.

2.4 Experimental Methods for Wildlife

The British Columbia Ministry of Environment donated carcasses of recently killed wildlife (Photograph 7). These were nuisance animals and are normally destroyed and incinerated (Forbes 1994). The species obtained were commonly poached animals and represented a rare research opportunity. Because carcasses were offered when they

TABLE 2. State of carrion, time of death, time of placement, and location of eight wildlife carcasses, 1994-1995.

SPECIES	IDENTIFICATION NUMBER	STATE OF CARCASS	DATE OF DEATH	SEASON OF PLACEMENT	BIOGEOCLIMATIC ZONE	HABITAT
Black bear	1	fresh	17-Aug-94	Summer	Coastal Western Hemlock	Sun
	2	fresh	20-Sep-94	Fall	Coastal Western Hemlock	Shade
	3	frozen	1994	Summer	Coastal Western Hemlock	Shade
Cougar	1	frozen	Jan-95	Summer	Sub-boreal Spruce	Sun
	2	frozen	Jan-95	Summer	Sub-boreal Spruce	Sun
	3	frozen	Jan-95	Summer	Sub-boreal Spruce	Sun
	4	frozen	1995	Winter	Coastal Western Hemlock	Shade
	5	frozen	1995	Winter	Coastal Western Hemlock	Shade

were available, no control over type, size, timing or number was possible. Three black bear (*Ursus americanus*) and five cougar (*Puma concolor*) carcasses (Table 2) were donated; one bear carcass could not be used because of insufficient cages and is not included in Table 2. The carcasses were received as available in different habitats, seasons and zones, making replication difficult. For this reason, the wildlife ancillary study coincided with that of pigs, and used the same experimental methods. However, because of the limited number and large size of wildlife carcasses, there were two differences in the protocol: the use of previously-frozen carcasses (seven of nine carcasses); and the use of large cages, strong mesh platforms, strong weighing tripod, and a heavy-duty scale to accommodate the large and heavy carcasses.

2.5 Categories of Decomposition

Goff's (1993) definitions of five decomposition stages were used, but modified to accommodate clothed pig and wildlife carcasses.

The ***Fresh Stage*** begins immediately following death and lasts until the first sign of bloating. Calliphoridae (blow flies) are the predominant insect species characterizing this stage. Clothing may retain fresh body fluid stains, depending on the length of the fresh stage in various seasons. Live ectoparasites such as ticks and fleas may be associated with animal fur.

The ***Bloat Stage*** begins with distension of the abdomen due to bacterial action in the gastro-intestinal tract. During the bloat stage, putrefaction, and insect metabolic and mechanical activity may act to increase internal carcass temperatures. Blow fly adults and larvae dominate the carcass. The presence of clothing or scavenging (Photograph 8) may affect this stage or mask observations.

The ***Decay Stage*** begins with the deflation of the bloated carcass. The skin is usually broken by calliphorid or sarcophagid feeding which allows gases to escape. Maggots feed actively on carrion during this stage and may create significant increases in internal carcass temperatures. Steam and foam may occur. This stage is complete when maggot feeding activity ceases, and maggots migrate. Clothing becomes oily,

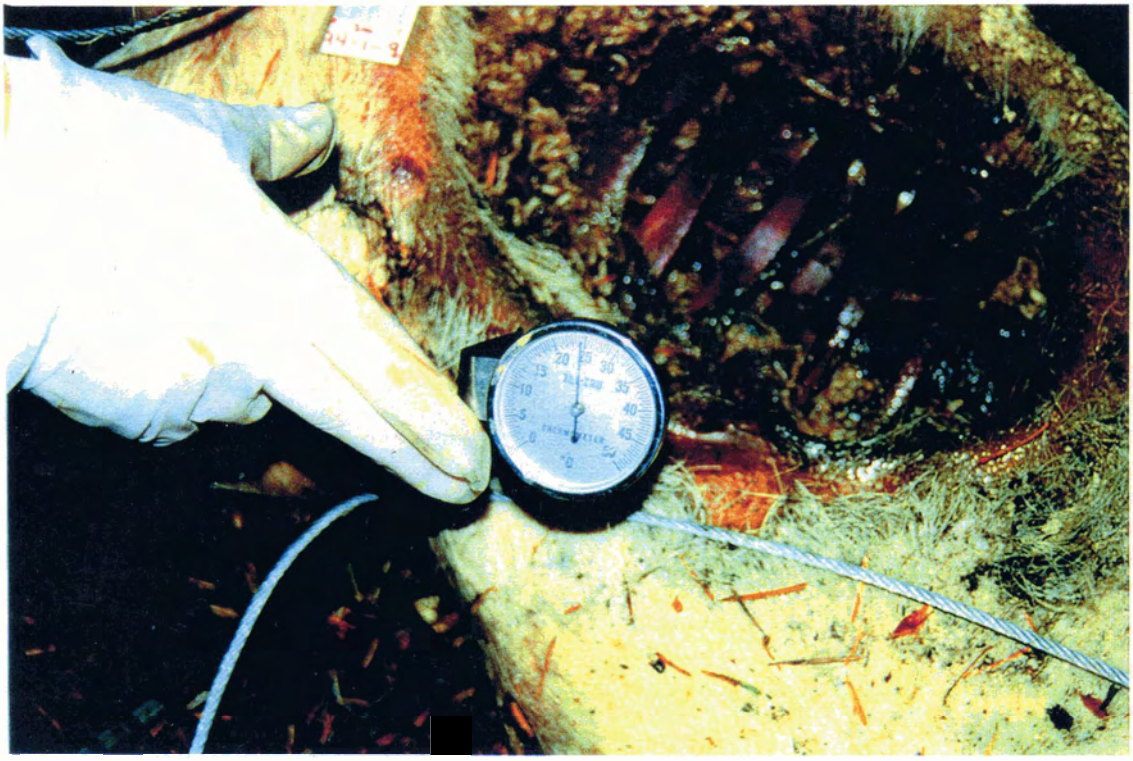
soaked and stained with body fluids, and may contain prepupal maggots and pupa (Photograph 9). Hair becomes detached from carcasses of wildlife (Photograph 10).

In the **Post-Decay Stage**, the carcass consists of fatty tissue, cartilage, skin and bones. Insect species inhabiting the carrion become diverse, as blow fly communities become replaced with various other insect communities. Degradation of clothing may begin.

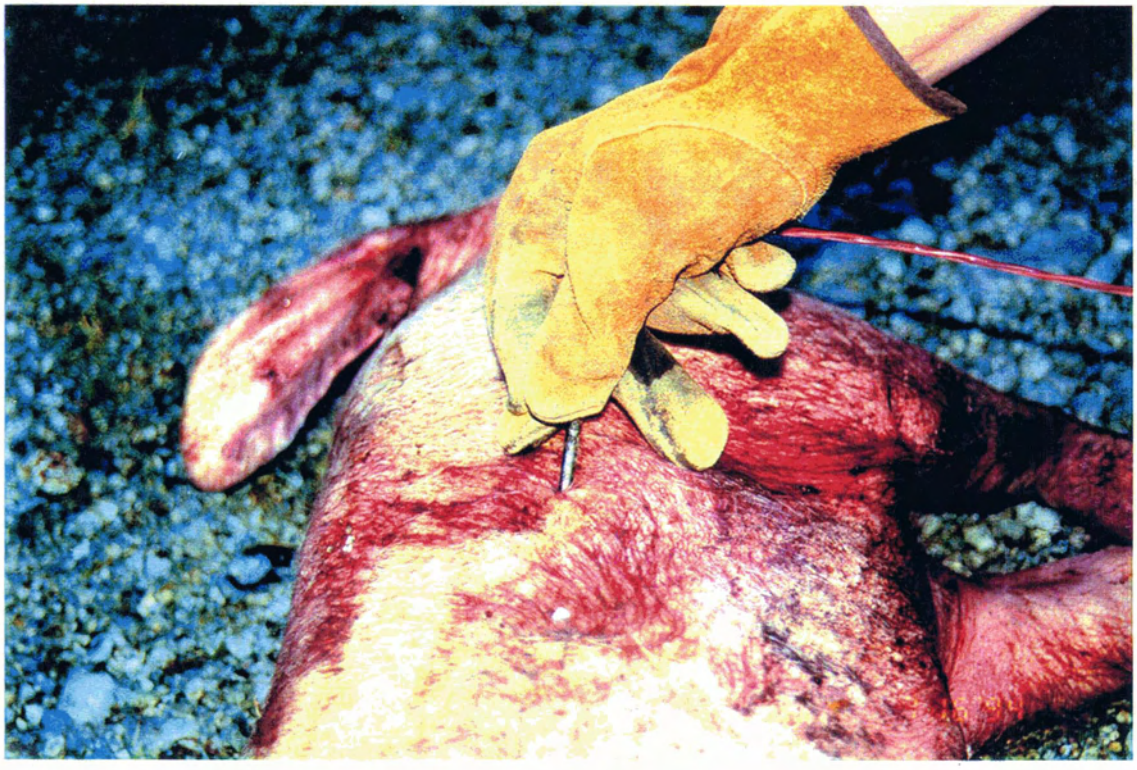
The final stage–***Remains Stage***–is reached when only hair, some skin and bones of the carcass remain. Few insects are associated with the carrion during this stage.

Photograph 1. Steel-barred cage used to house a pig carcass

Photograph 2. Weighing equipment



Photograph 3. Hand-held thermometer

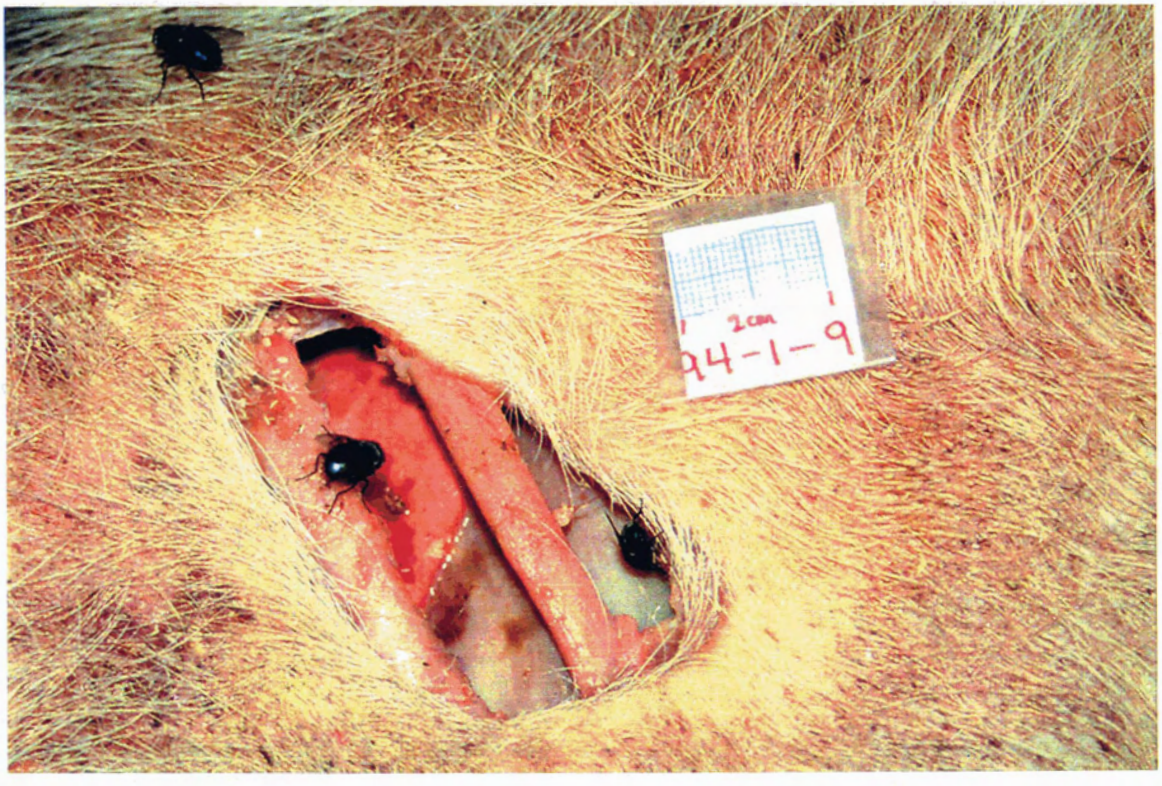


Photograph 4. Temperature probe.

Photograph 5. Datalogger (Smartreader 1®) downloading.

Photograph 6. Blowfly larval activity within clothing.

Photograph 7. Black bear carcass



Photograph 8. Bullet wound enlarged by scavenging

Photograph 9. Prepupal larvae and pupae within clothing.

Photograph 10. Fur detached from cougar carcass.

3. RESULTS

Control and experimental pig carcasses did not appear to differ in decomposition characteristics or insect activity. Therefore, periodic disturbance of the experimental carcasses potentially did not bias my experiments. Based on this finding, all insect observations and collection data obtained from experimental and control carcasses within the same experimental set were pooled and analyzed together. Observations were made on a limited number of wildlife carcasses, without control carcasses, as a pilot study.

3.1 Decomposition

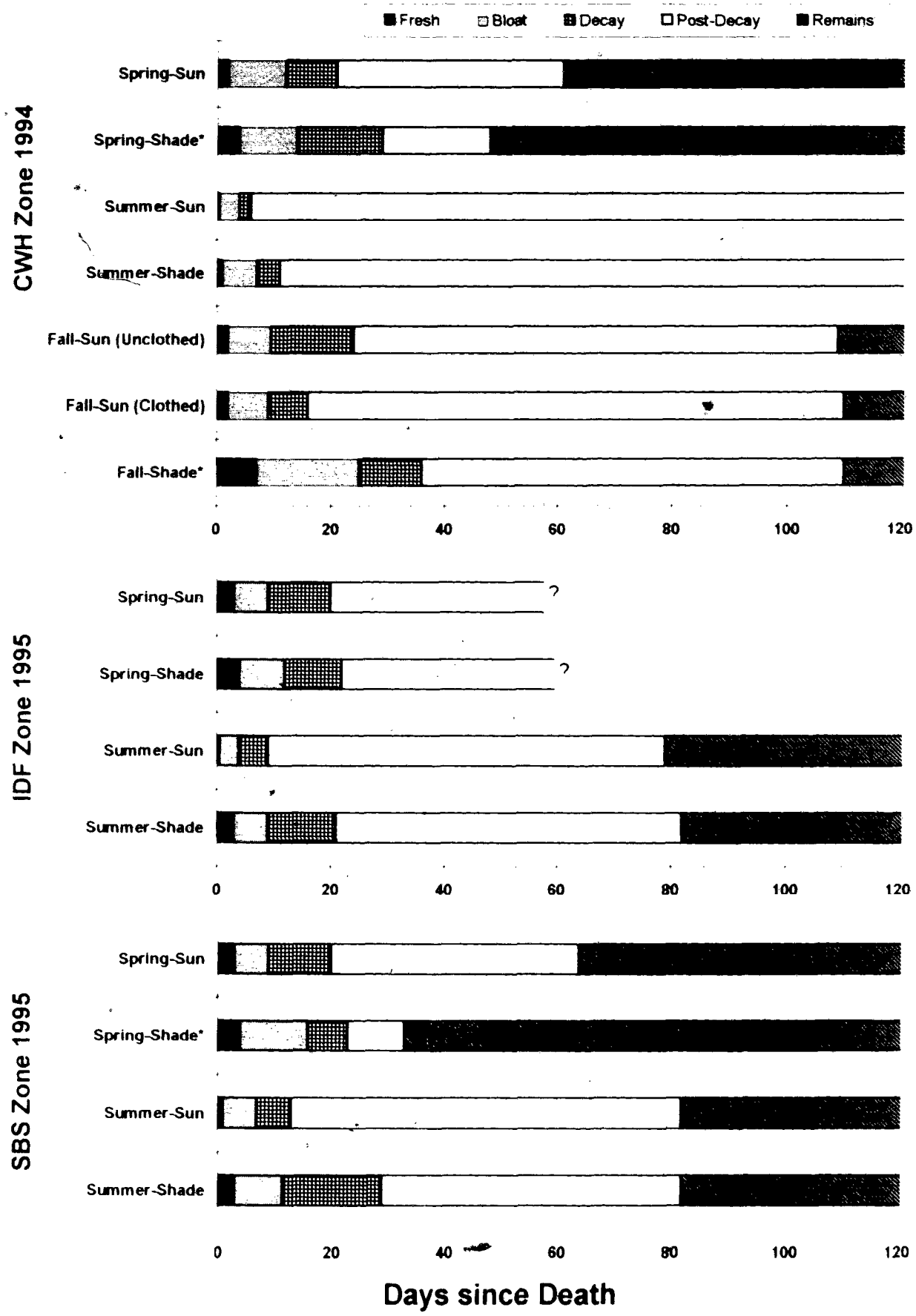
Decomposition followed Goff's (1993) five stages: fresh, bloat, decay, post-decay, and remains. The higher the ambient temperature of a habitat, season, or zones, the shorter the decay stage and the faster a pig carcass progressed through the various stages of decomposition (Figure 4). Clothing increased the rate of decomposition and masked the beginning and end of the bloat stage, making it difficult to visually assess transitions. Patterns of decomposition for fresh wildlife carcasses were similar to those for pig carcasses located in the same habitat, season and zone but of longer duration (Figure 5).

Scavenging by vertebrates increased the speed of decomposition or eliminated some decompositional stages in both pig and wildlife carrion. Scavenging varied with habitat, season, and zone. Scavenging did not occur during summer, was infrequent in sun habitats, and was not observed in the IDF zone.

Weight loss for unclothed pig carcasses was more rapid in sun than in shade, and was most rapid during summer and slowest during fall (Figure 6). In three instances, rainfall absorbed by pig carrion tissue increased their weight slightly during spring. However, these temporary increases were small and weight declined with days since death. Weight measurements for clothed pig carrion were not reliable indicators of the rate of decomposition because clothing gained and lost moisture sporadically over time (Figure 7).

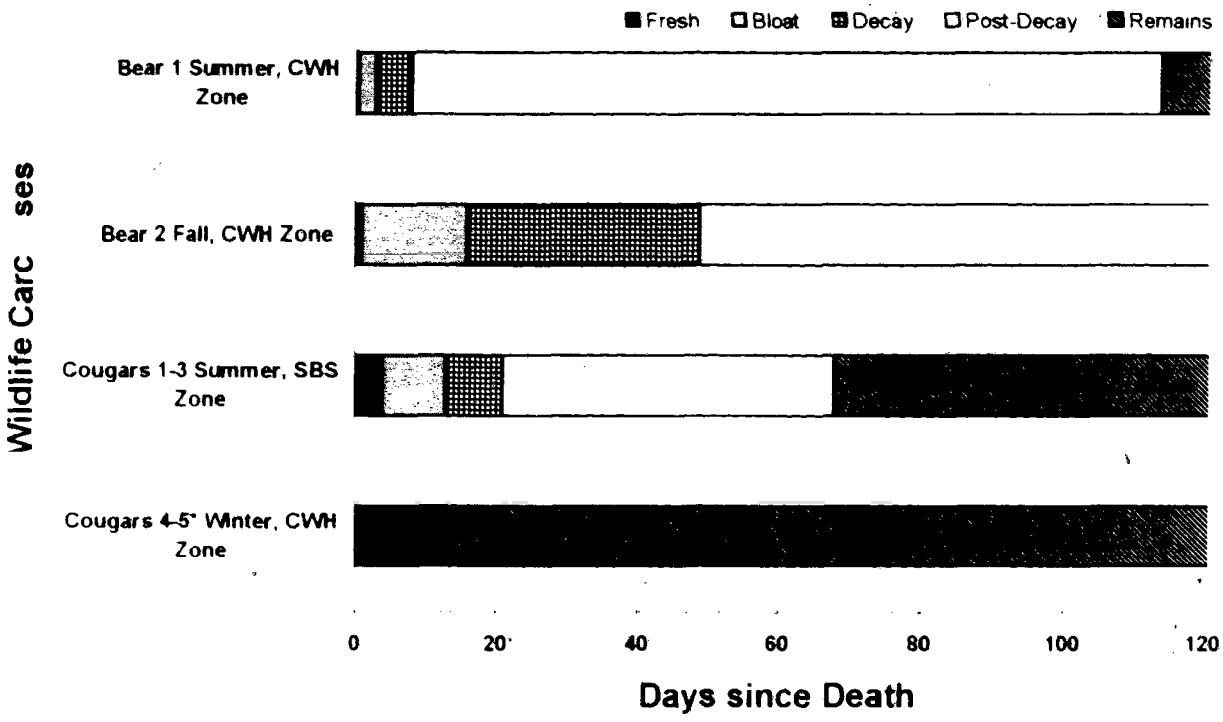
Initially, weight loss of wildlife carcasses (Figure 8) was similar to that of clothed pig carrion (Figure 6 and 7). Animal hair, like clothing, absorbed rain, and influenced weight measurements. Because hair fell off wildlife carcasses during the decay stage, by the post-decay stage, rain did not influence weight. Despite these influences, weight declined with increasing time since death, similar to unclothed carcasses (Figure 6).

Figure 4. Mean duration of decay stages of pig carcasses (n = 5 with exception of fall-sun (clothed) bar where n = 2) during 1994-1995 in three biogeoclimatic zones. The end of the post-decay stage during spring in the Interior Douglas-fir (IDF) zone (marked with a question mark) was not observed. All pig carcasses in the IDF and Sub-Boreal Spruce (SBS) zones were clothed.



*Decay stages affected by scavenging.

Figure 5. **Duration of decay stages for Bear 1, 2 and mean duration of decay stages for Cougars 1-5 during 1994-1995 in two biogeoclimatic zones. Bear carcasses were received fresh, cougar carcasses were received frozen.**



*Cougars 4 and 5 were heavily scavenged during the fresh stage.

Figure 6. Mean percent weight of unclothed (n = 3) (carcass #1-30) and clothed (carcass #31 and 32) pig carcasses, in sun and shade and daily rainfall for spring, summer, and fall in the Coastal Western Hemlock (CWH) biogeoclimatic zone during the fresh, bloat and decay stages of decomposition only. Rainfall measurements provided by Environment Canada (1994). See Table 1 for dates of day zero.

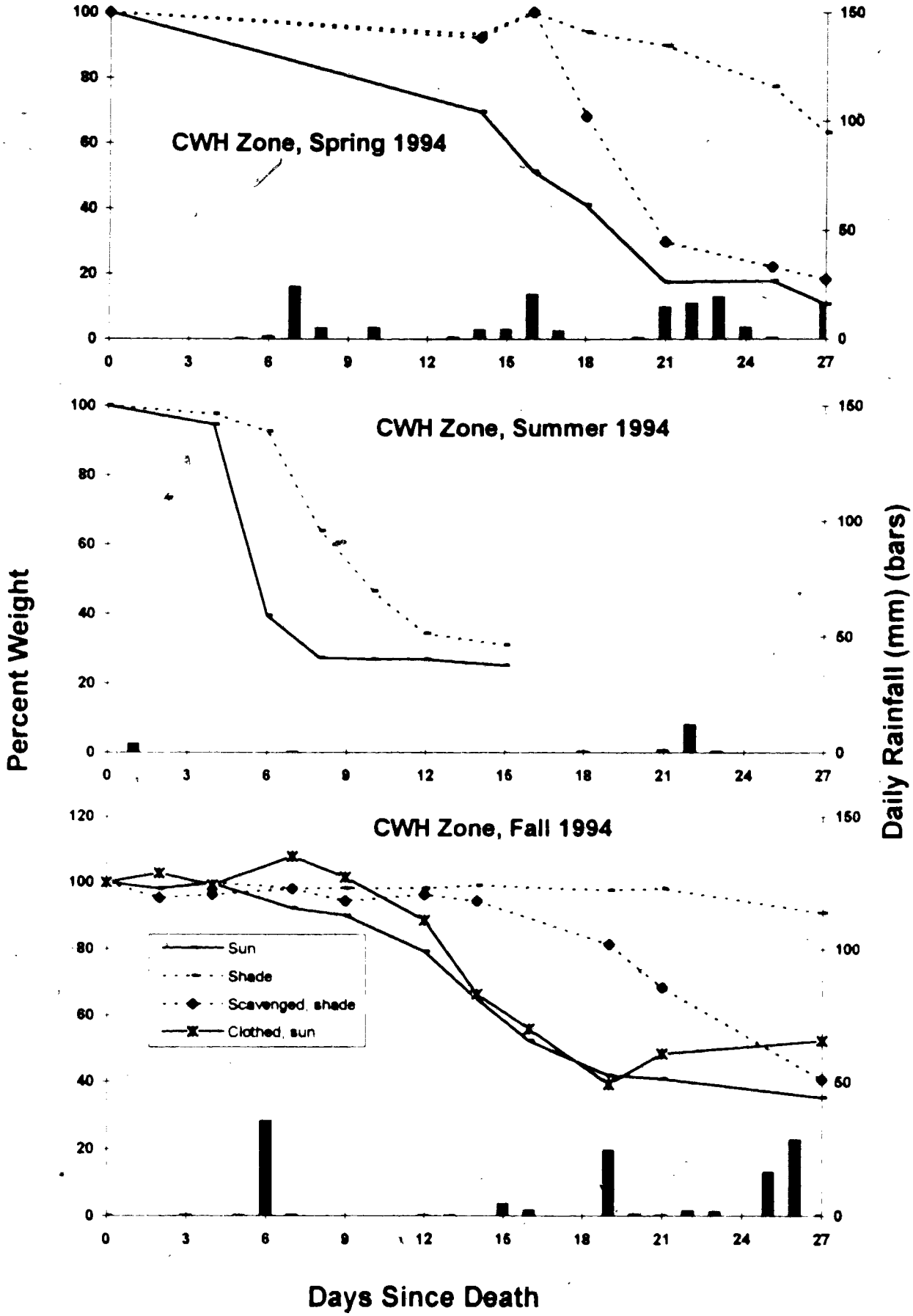

CWH Zone, Spring 1994
CWH Zone, Summer 1994
CWH Zone, Fall 1994
Percent Weight
Daily Rainfall (mm) (bars)
Days Since Death
Sun
Shade
Scavenged, shade
Clothed, sun

Figure 7. **Mean percent weight of clothed pig carcasses (n = 3) (IDF #33-52; SBS #53-72) in sun and shade and daily rainfall for spring, and summer in the Interior Douglas-fir (IDF) and Sub-Boreal Spruce (SBS) biogeoclimatic zones during the fresh, bloat and decay stages of decomposition only. Rainfall measurements provided by Environment Canada (1995). See Table 1 for dates of day zero.**

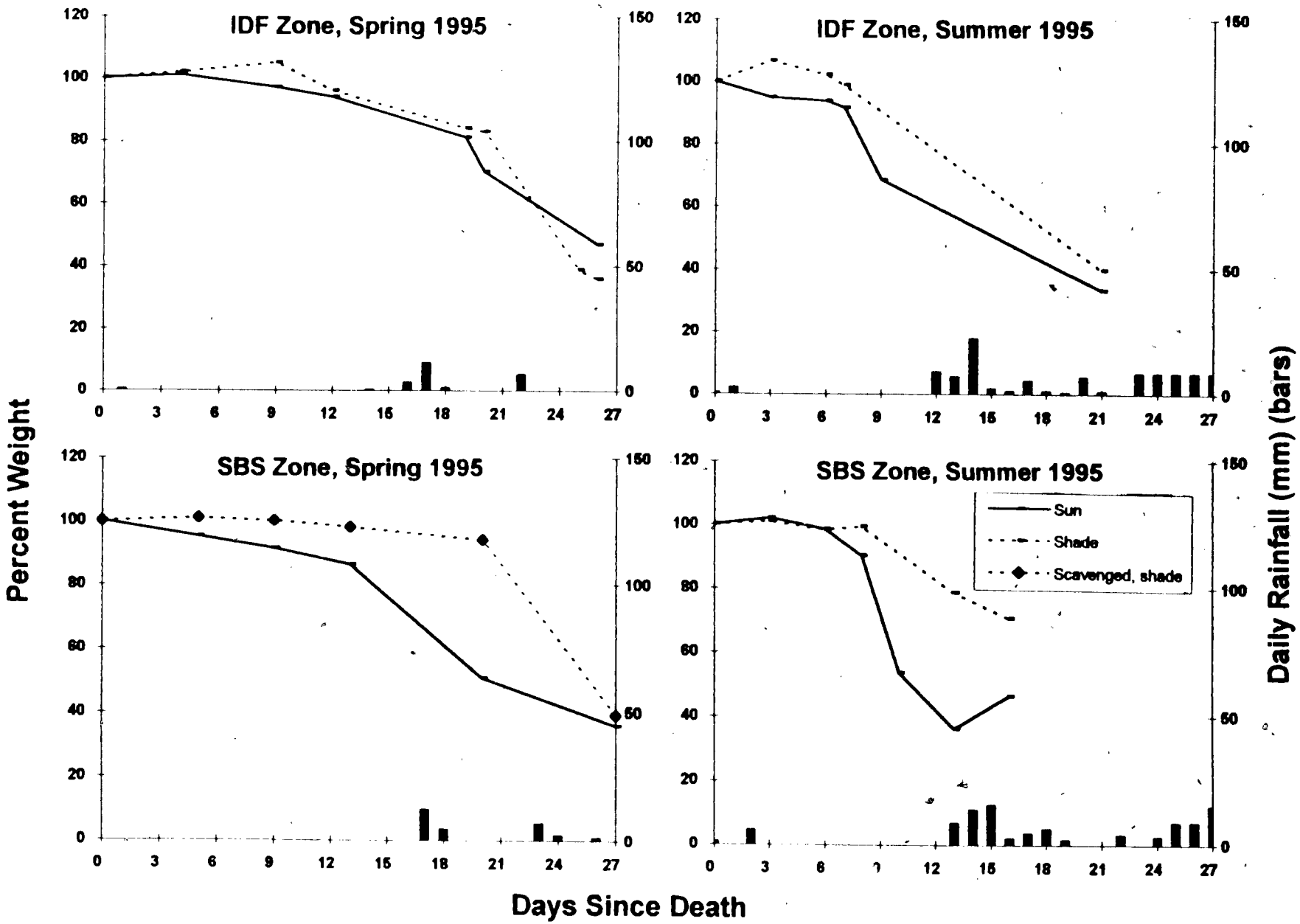
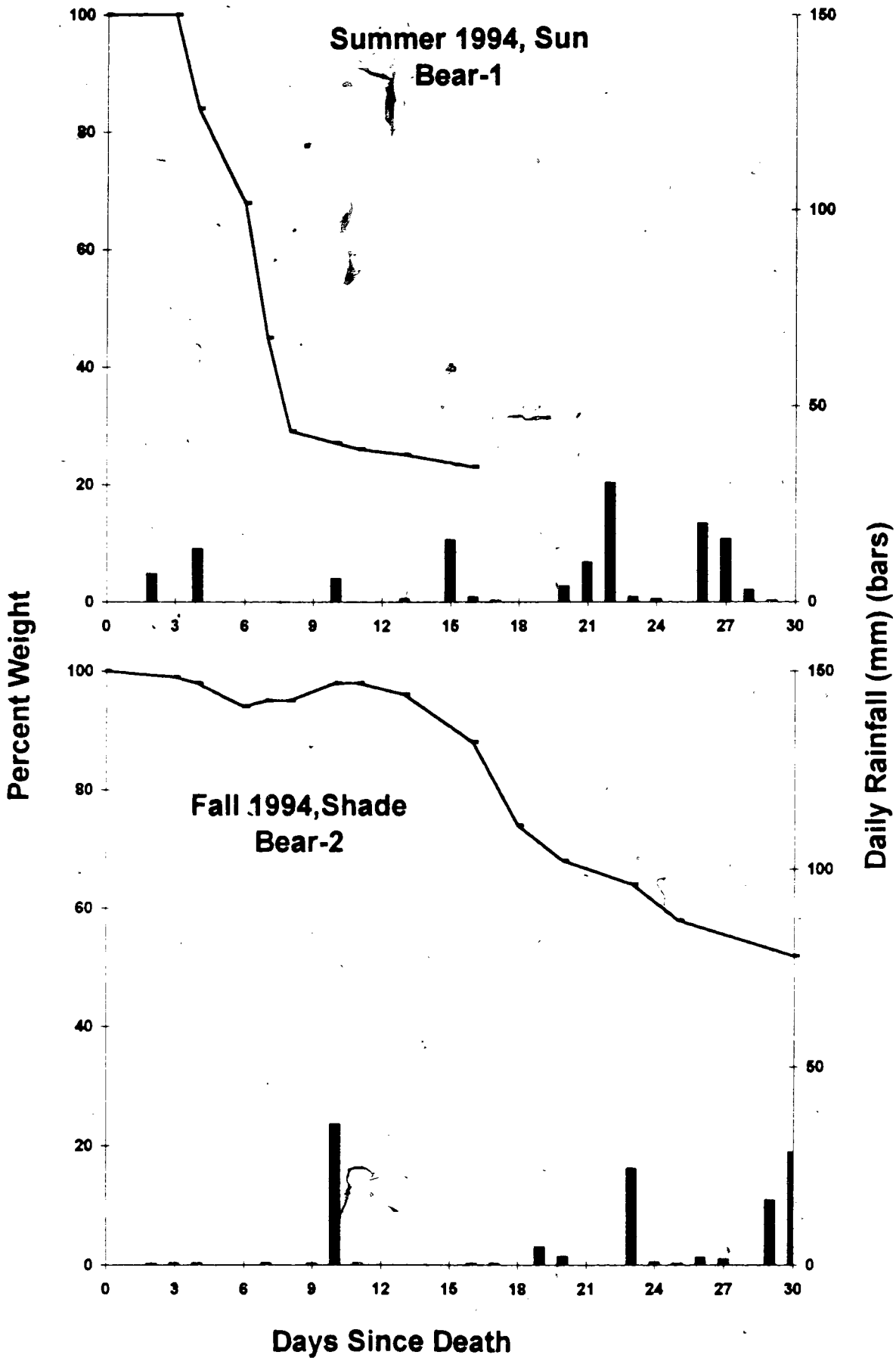

IDF Zone, Spring 1995
IDF Zone, Summer 1995
SBS Zone, Spring 1995
SBS Zone, Summer 1995
Sun
Shade
Scavenged, shade
Percent Weight
Daily Rainfall (mm) (bars)
Days Since Death

Figure 8. **Percent weight loss in 1994 for Bear 1 in sun during summer and Bear 2 in shade during fall and corresponding daily rainfall in the Coastal Western Hemlock (CWH) biogeoclimatic zone during the fresh, bloat and decay stages of decomposition only. Rainfall measurements provided by Environment Canada (1994). See Table 2 for dates of day zero.**


Summer 1994, Sun
Bear-1
Fall 1994,Shade
Bear-2
Percent Weight
Daily Rainfall (mm) (bars)
Days Since Death
100
80
60
40
20
0
150
100
50
0
3
6
9
12
15
18
21
24
27
30

In shade, scavenged pig carrion lost mass faster than did unscavenged carrion (Figures 6 and 7), apparently through consumption of tissue by scavengers. Scavengers removed both tissue and associated clothing from carcasses. During spring and fall, weight loss of scavenged pig carcasses in shade was similar to that of unscavenged pig carcasses in sun. Initially frozen cougar carcasses (Cougars 4 and 5) did not decompose during winter, but they were heavily scavenged and as a result, rapidly reached the remains stage.

3.2 Insect Activity

3.2.1 Blow Fly Development

Behaviour and biology of blow flies were similar for pig and wildlife carrion (Tables 3 and 4). The blow fly species were all common to rural habitats in British Columbia: *Calliphora vomitoria* (L.); *Lucilia illustris* (Meigen); *Phormia regina* (Meigen); and *Protophormia terraenovae* (Robineau-Desvoidy). All four species were attracted to and reproduced successfully on both pig and wildlife carrion in specific habitats, seasons and biogeoclimatic zones. Blow flies, such as *Phaenicia sericata* (Meigen) and *Calliphora vicina* (Robineau-Desvoidy), which are typical of urban areas in B.C., were not observed on any of the carcasses.

Habitat and season influenced the number of blow flies and diversity of blow fly species in the CWH zone, resulting in complex, inter-related observations in the CWH zone. No habitat or seasonal differences in the number of blow flies or diversity of blow fly species occurred in the IDF or SBS zones. Oviposition by calliphorids occurred on most pig and wildlife carrion within minutes to hours after death in sun and shade during all seasons in the CWH zone. Oviposition on spring carcasses in both IDF and SBS zones was not observed until the second day after death regardless of habitat. However, once the blow fly eggs hatched, the larvae successfully colonized the carcasses. Adult blow flies and their larvae were not observed on two cougar carcasses (Cougar 4 and 5) placed in the CWH zone during winter.

Different patterns of oviposition occurred on clothed and unclothed pig carcasses. On unclothed pig carcasses in both sun and shade, blow fly eggs were deposited in clusters within moist and unexposed areas such as facial and anogenital orifices, wound sites and at ground-skin interfaces. In shade, blow flies also deposited eggs on dry, exposed skin surfaces, however high egg mortality occurred, probably due to egg desiccation.

Table 3. Summary of blow fly development observations from 72 pig carcasses in three biogeoclimatic zones.

OBSERVATIONS	ZONES* CWH	IDF	SBS
Colonization by rural blow fly species only	YES	YES	YES
Sites of oviposition differed between sun and shade	YES	NO	NO
Oviposition occurred immediately during spring in both sun and shade	YES	NO	NO
Oviposition occurred immediately during summer in both sun and shade	YES	YES	YES
Oviposition occurred immediately during fall in both sun and shade	YES	N/A	N/A
Rainfall reduced adult calliphorid activity, sun habitats only	YES	YES	YES
Calliphorid larvae did not live continuously at maximum internal temperatures	YES	YES	YES
Larvae moved in and out of masses and to various sites on carrion	YES	YES	YES
Temperatures of various maggot masses on the same carcass differed by as much as 10°C	YES	YES	YES
During summer, and during bloat and decay, maggot mass temperatures measured during sampling periods corresponded closely to maximum internal temperatures	YES	YES	YES
Internal carcass temperatures peaked earlier in sun than in shade	YES	YES	YES
During summer, migration occurred due to lack of food rather than larval developmental stage	YES	NO	NO
In shade habitats, oldest prepupal larvae migrated before peak internal temperatures	YES	YES	YES
Undersized puparia and adults occurred when larval population densities were very high	YES	NO	NO

* YES = Observed. NO = Not observed. N/A = Not applicable–not included in research design.

Table 4. Summary of blow fly development observations from seven wildlife carcasses. Cougars 4 and 5 were placed in winter and heavily scavenged.

	CARRION OBSERVED*			
OBSERVATIONS	**Bear 1**	**Bear 2**	**Cougar 1-3**	**Cougar 4,5**
Colonization occurred by rural blow fly species only	YES	YES	YES	N/A
Oviposition occurred immediately	YES	YES	YES	NO
Hair on carrion did not impede oviposition	YES	YES	YES	N/A
Adults deposited eggs on blood-soaked hairs near wounds	YES	YES	YES	NO
First instars migrated down blood-soaked hairs toward wound sites	YES	YES	YES	NO
Calliphorid larvae did not live continuously at maximum internal temperatures	YES	YES	N/A	N/A
Larvae moved in and out of masses and to various sites on carrion	YES	YES	YES	N/A
Temperatures of various maggot masses on the same carcass differed by as much as 10°C	YES	YES	N/A	N/A

* YES = Observed. NO = Not observed. N/A = Not applicable–not included in research design.

Clothing on pig carcasses absorbed and retained body fluids, which made them more attractive to insects. Eggs were deposited in moist crevices provided by clothing, as well as along collars, waist bands and on blood-soaked material. Successful hatching occurred at these additional sites, creating considerable larval aggregations. Blow fly larvae were observed under skin and clothing. Maggot movement in all pig carcasses was sufficiently intense to move temperature probes close to the surface as well as from deep within a maggot mass, to displace small bones and to undulate carrion skin, and clothing.

On wildlife carcasses, calliphorid flies were attracted mainly to the multiple wound sites. Eggs were laid not on the tissue surrounding the wound, as on pig carcasses, but rather on blood soaked hairs located within 10 cm of the wound site. Newly emerged first instar larvae were observed to migrate down shafts of hair toward the wound site. Intense maggot movement was sufficient to move and undulate animal fur.

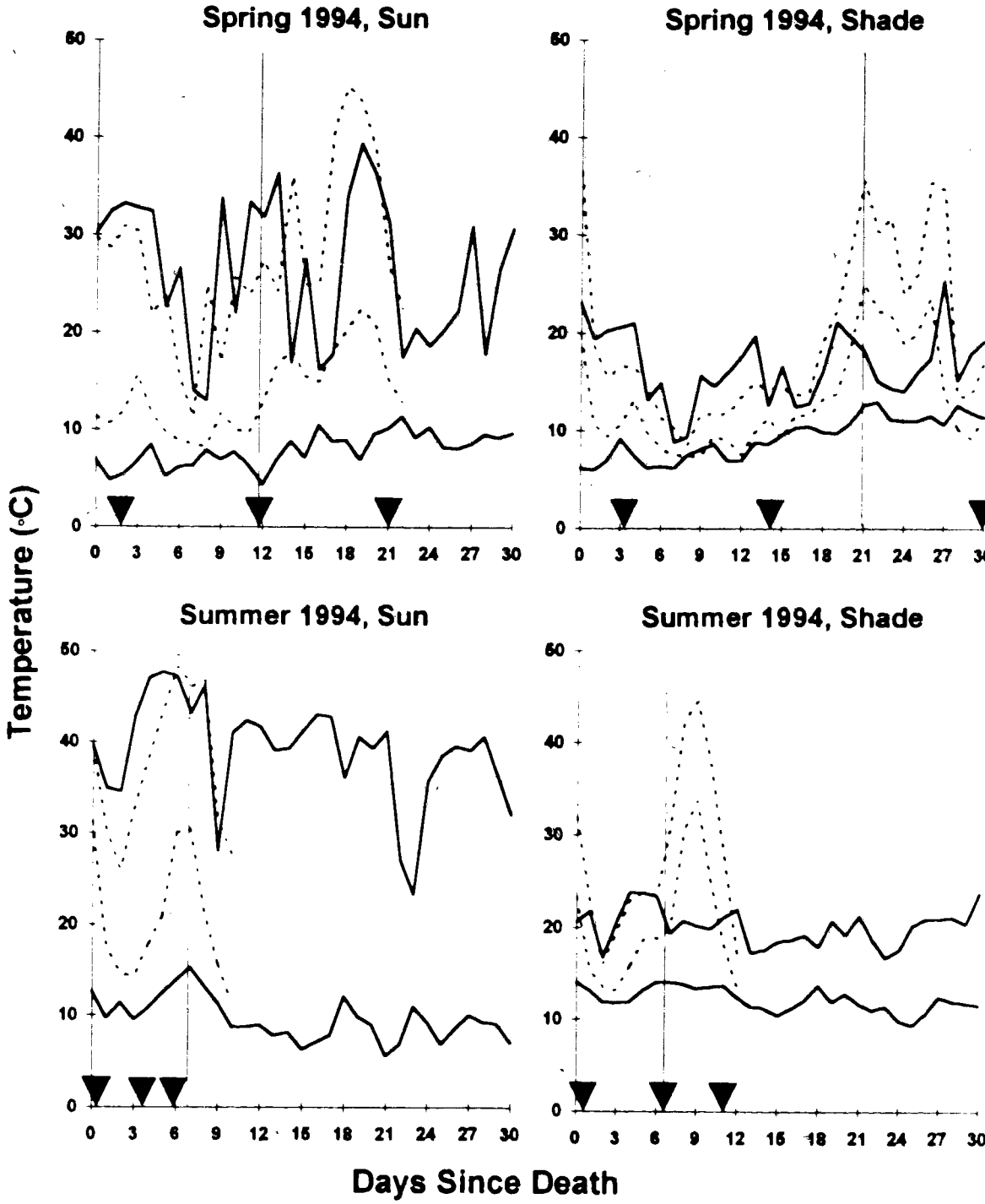
During fall in the CWH zone, when average ambient temperatures were low (Figure 9), there was high mortality of larvae on both pig and wildlife carcasses. Few larvae pupated and some may have entered diapause. Blow fly larvae from wildlife carcasses pupated not only in surrounding soil and debris but also within mats of hair on or near the carcass.

Internal temperatures of pig carcasses showed diurnal temperature changes and increased after maggot masses coalesced. The timing of peak internal pig carcass temperatures, reflecting main activity of maggot masses, occurred earlier in carcasses that were in sun than those in shade, and in carcasses placed during summer than those placed during spring or fall (Figures 9-11). Maggot masses reached similar peak internal temperatures in both sun and shade. However, in shade, the oldest prepupal larvae migrated before peak internal temperatures were reached.

Temperatures of established maggot masses in experimental pigs were similar to the maximum internal carcass temperatures recorded by dataloggers in control carcasses during summer, but generally fell between the maximum and minimum internal carcass temperatures during spring and fall (Figure 12). Correlations were examined between ambient and internal carcass temperatures during the bloat and decay stages (Table 5). In general, there were stronger correlations ($P<0.05$) between ambient and internal temperatures during the bloat stage than in comparison with the decay stage ($P<0.05$).

In the CWH zone, during summer, all experimental sites located in sun, experienced ambient temperatures above 25°C. Such temperatures lead to fast development rates in blow fly larvae resulting in competition among larval stages for food resources. This competition

Figure 9. Daily maximum and minimum mean ambient and internal pig carcass (n = 2) temperatures in sun or shade for three seasons in the Coastal Western Hemlock (CWH) biogeoclimatic zone. Arrows on X axis indicate transition between fresh, bloat, decay and post-decay stages. Vertical line indicates date of migration of oldest calliphorid prepupal larvae. See Table 1 for dates of day zero.


Spring 1994, Sun
Spring 1994, Shade
Summer 1994, Sun
Summer 1994, Shade
Temperature (°C)
Days Since Death
0
10
20
30
40
50
0 3 6 9 12 15 18 21 24 27 30

Continued Figure 9.

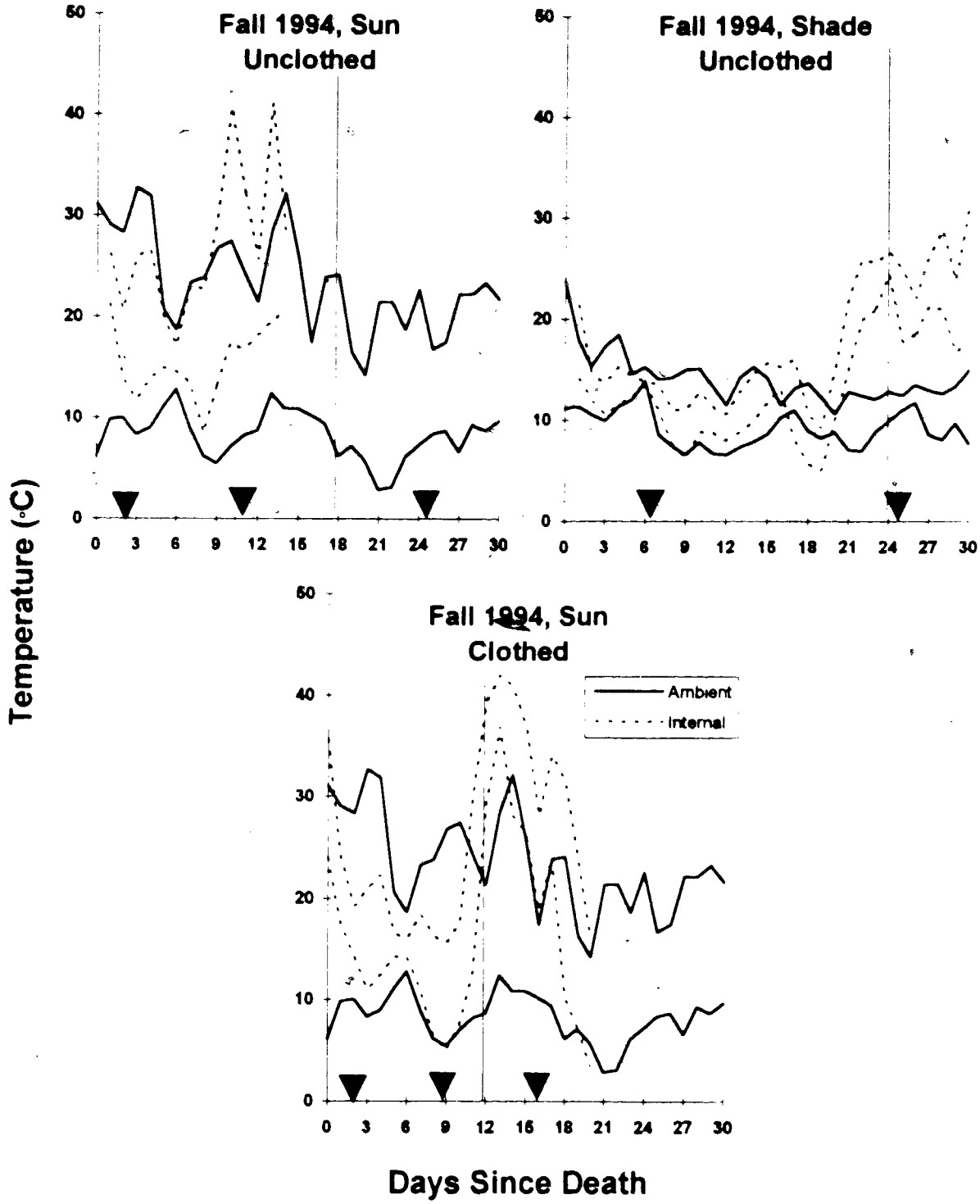


Figure 10. Daily maximum and minimum mean ambient and internal pig carcass (spring n = 2, summer n = 1) temperatures in sun or shade for two seasons in the Interior Douglas-fir (IDF) biogeoclimatic zone. Arrows on X axis indicate transition between fresh, bloat, decay and post-decay stages. Vertical line indicates date of migration of oldest calliphorid prepupal larvae. See Table 1 for dates of day zero.

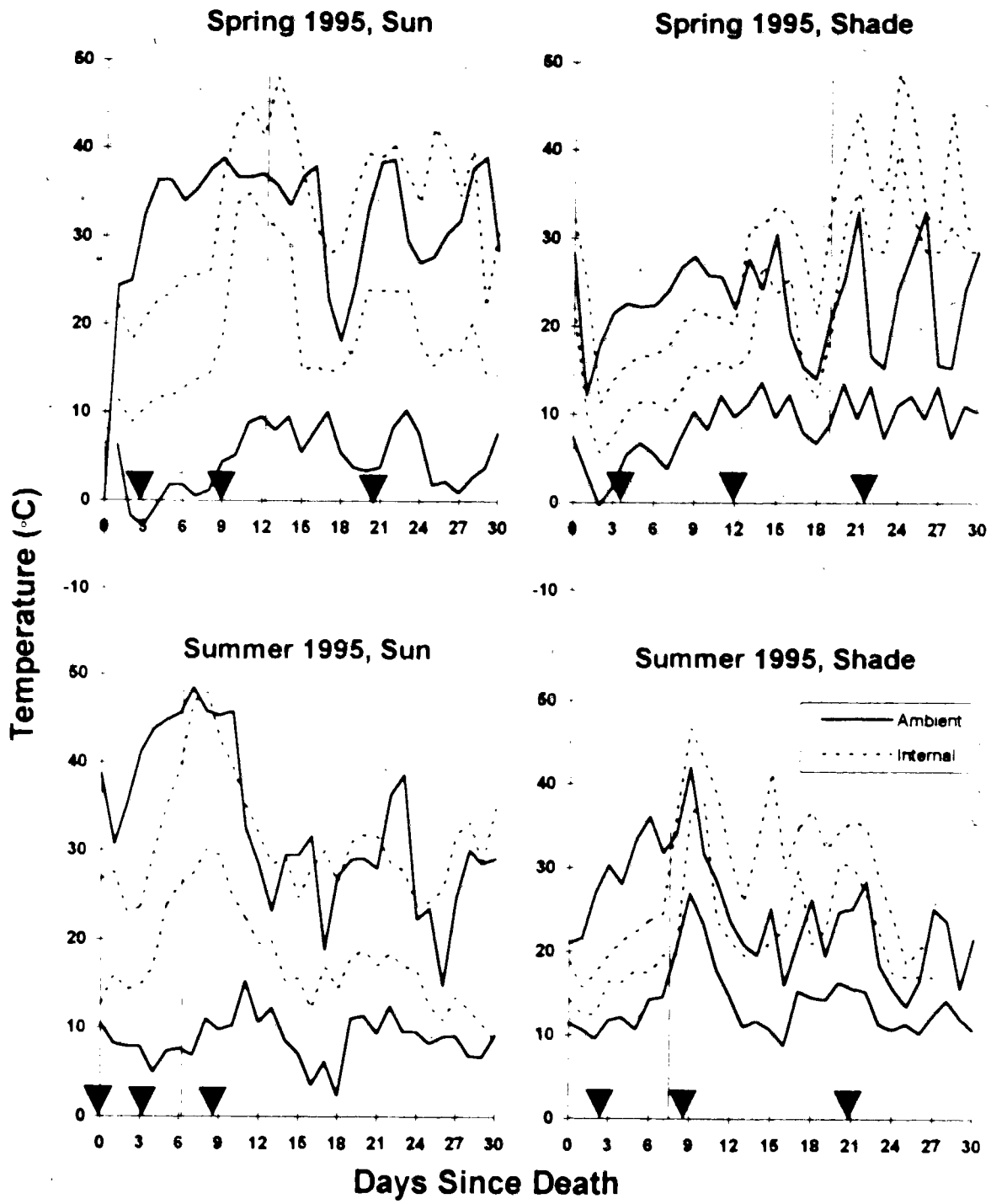

Spring 1995, Sun
Spring 1995, Shade
Summer 1995, Sun
Summer 1995, Shade
Ambient
Internal
Temperature (°C)
Days Since Death

Figure 11. Daily maximum and minimum mean ambient and internal pig carcass (n = 2) temperatures in sun or shade for two seasons in the Sub-Boreal Spruce (SBS) biogeoclimatic zone. Arrows on X axis indicate transition between fresh, bloat, decay and post-decay stages. Vertical line indicates date of migration of oldest calliphorid prepupal larvae. See Table 1 for dates of day zero.

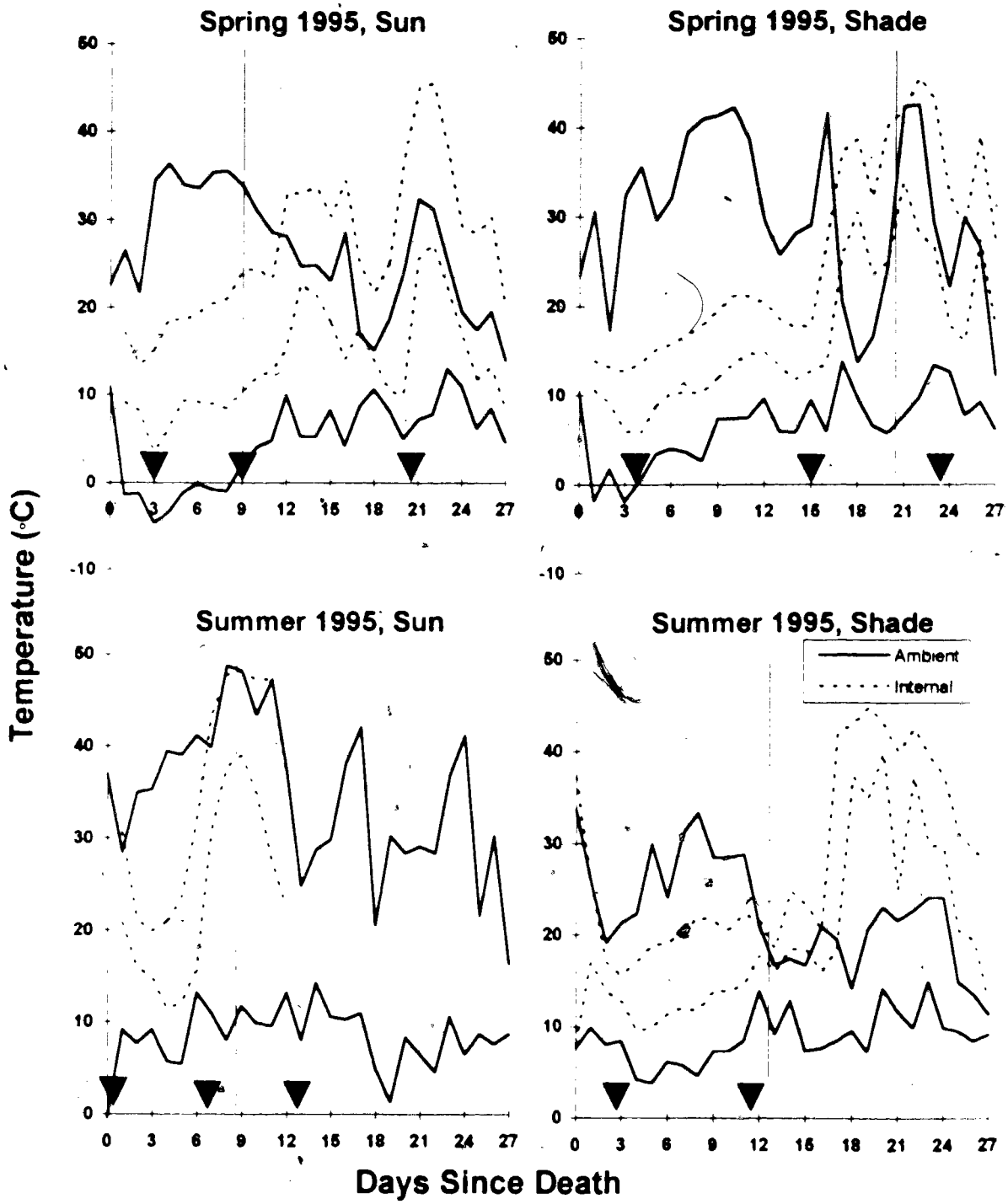

Spring 1995, Sun
Spring 1995, Shade
Summer 1995, Sun
Summer 1995, Shade
Ambient
Internal
Temperature (°C)
Days Since Death

Figure 12. Daily maximum and minimum mean internal temperatures from control carcasses (n = 2) and maggot mass temperatures (diamonds) from experimental carcasses (n = 3) in the sun and shade during the bloat and decay stages during spring, summer and fall 1994, in the CWH biogeoclimatic zone. Arrows on X axis indicate transition between fresh, bloat, decay and post-decay stages. See Table 1 for dates of day zero.

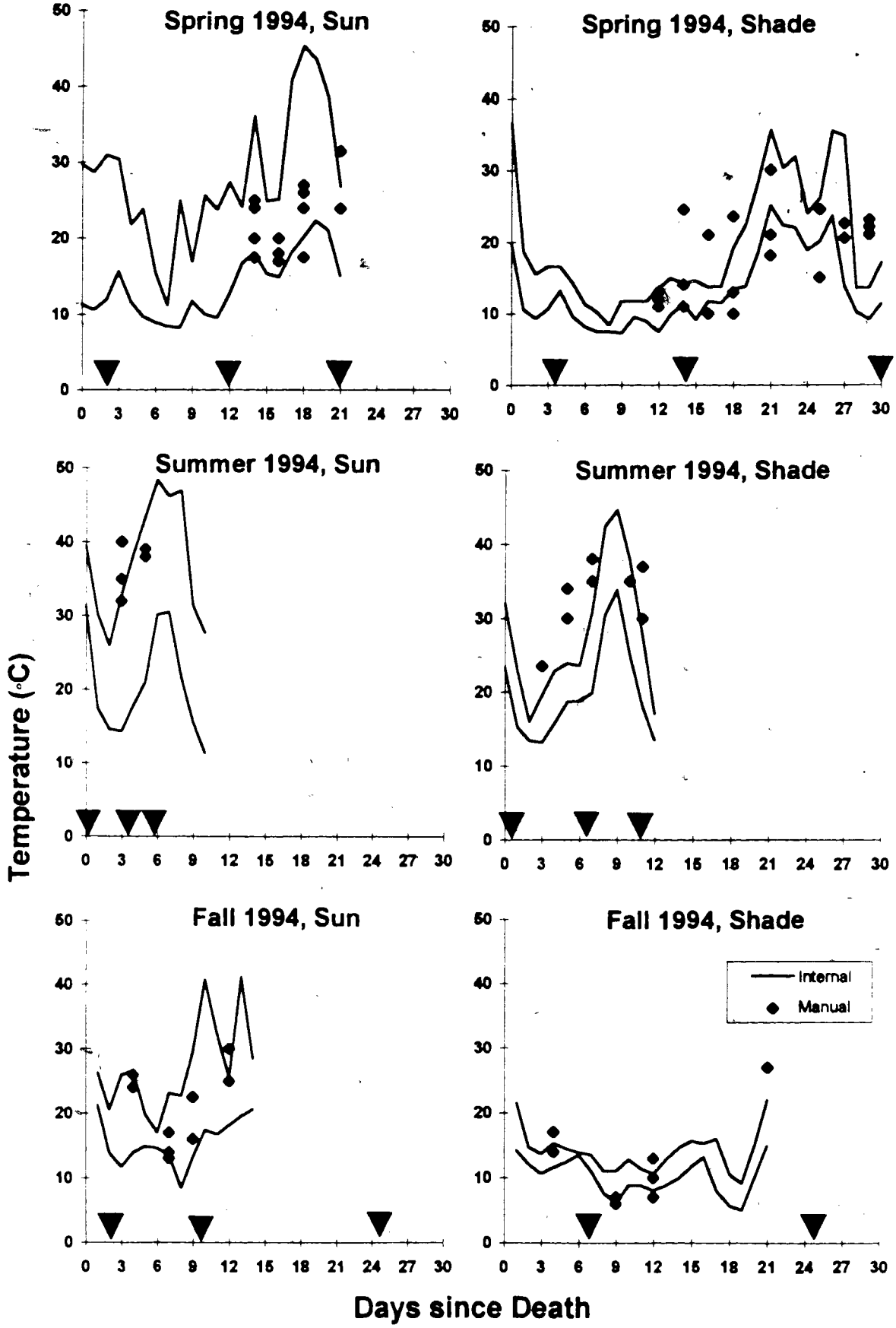

Spring 1994, Sun
Spring 1994, Shade
Summer 1994, Sun
Summer 1994, Shade
Fall 1994, Sun
Fall 1994, Shade
Internal
Manual
Temperature (°C)
Days since Death

Table 5. Regression statistics between maximum, minimum and mean ambient (independent x variable) and internal (dependent y variable) temperatures of pig carcasses during the bloat and decay stages in three biogeoclimatic zones. Only significant regressions are shown (P<0.05). Applicable for ambient temperature ranges of 5°C to 50°C for Coastal Western Hemlock (CWH) zone, 0°C to 50°C for Interior Douglas-fir (IDF) zone, -5°C to 50°C for Sub-Boreal Spruce (SBS) zone.

Zone	Season	Decay Stage	Habitat	Temperature	Regression Equation	r^2	P
CWH	spring	bloat	sun	mean	y = 0.84x + 2.75	0.73	<0.01
			shade	max	y = 0.46x + 5.78	0.56	<0.01
				mean	y = 0.64x + 3.81	0.46	0.02
		decay	sun	mean	y = 1.04x + 5.79	0.49	0.02
	summer	bloat	shade	min	y = 2.34x - 13.6	0.77	<0.01
				mean	y = 0.76x + 5.46	0.85	<0.01
	fall	bloat	sun (clothed)	max	y = 0.39x + 8.08	0.65	0.02
				min	y = 1.38x - 1.31	0.87	<0.01
		decay	sun (clothed)	min	y = 4.60x - 22.10	0.70	0.02
IDF	spring	bloat	sun	min	y = 1.02x + 12.48	0.69	0.02
				mean	y = 1.67x - 11.01	0.73	0.01
			shade	max	y = 0.84x + 1.36	0.60	0.01
				min	y = 0.82x + 6.76	0.89	<0.01
		decay	sun	max	y = 0.59x + 19.01	0.39	0.03
				mean	y = 1.14x + 8.39	0.36	0.04
			shade	min	y = 2.12x + 0.17	0.42	0.03
				mean	y = 1.68x + 5.09	0.57	<0.01
	summer	bloat	shade	max	y = 1.84x - 34.06	0.69	0.02
				min	y = 1.10x + 3.07	0.81	<0.01
				mean	y = 1.64x - 16.37	0.94	<0.01
		decay	sun	min	y = 2.01x + 9.72	0.78	0.02
				mean	y = 4.10x - 76.97	0.99	<0.01
			shade	max	y = 0.74x + 17.31	0.72	<0.01
				min	y = 1.05x + 9.67	0.71	<0.01
				mean	y = 0.84x + 13.77	0.77	<0.01
SBS	spring	bloat	sun	min	y = 1.02x + 9.37	0.87	<0.01
				mean	y = 2.48x - 27.60	0.94	<0.01
			shade	min	y = 0.84x + 6.93	0.78	<0.01
				mean	y = 0.51x + 4.78	0.32	0.04
	summer	bloat	shade	max	y = 0.45x + 7.32	0.65	<0.01
				min	y = 0.89x + 6.67	0.78	<0.01
				mean	y = 0.75x + 3.29	0.72	<0.01
		decay	sun	max	y = 0.85x + 7.62	0.79	0.02

led to the inability for dipteran larvae to obtain adequate food because food resources were exhausted prior to the end of larval development.

Internal temperatures of wildlife carcasses was similar to maximum ambient temperatures during the fresh, and bloat stages (Figure 13). As for pig carcasses, internal carcass temperatures increased after maggot masses became established and the carcasses showed diurnal temperature changes.

3.2.2 Insect Succession

General observations on successional insects attracted to pig and wildlife carrion are summarized in Tables 6 and 7. Carrion insects collected from pig and wildlife carcass experiments included a total of 38 families and 56 genera (Tables 8-11), confirmed by Biosystematic Research Institute, Ottawa, Ontario. At the time of this writing, species identifications for many dipterans were not confirmed, hence species identifications were not included. Arachnids, acarina and incidental insect species were not included in the count.

Times of arrival, duration of stay, diversity and activity of insects occurred in patterns that varied with habitat, season, zone and factors such as size of carrion, scavenging by small vertebrates and presence of clothing or animal hair. Calliphorids dominated during the first three stages of decomposition. During the fourth stage, post-decay, successional insects in families such as Cleridae, Dermestidae, Fanniidae and Piophilidae dominated carrion. Colonization by most successional insects occurred earliest in warm habitats and warm seasons. The presence of moisture encouraged insect colonization by some species and discouraged others.

Clothing resulted in a greater diversity of successional insects on carcasses. For carcasses in the sun during the fall, important successional insect species, such as Fanniidae and Piophilidae, were on clothed but not on unclothed carcasses. Calliphorid larvae fed upon skin tissue covered by clothing. Exposed, unclothed skin tissue such as in the facial region was largely ignored until late stages of decay.

Animal hair absorbed moisture which faciliated larval feeding and provided protected sites for insect activity. This was true even after the hair detached from the carcass during the decay stage. Bear carcasses attracted a greater diversity of insects than did unclothed, furless pig carcasses in the same habitat, season, and zone. A comparison between cougar carcasses and clothed pig carcasses did not show these differences. Despite increased diversity of insects attracted to clothed or furred carcasses, the times of arrival for several insect species were very similar.

Figure 13. Daily maximum and minimum mean ambient and internal carcass temperatures of Bears 1 and 2 in the CWH biogeoclimatic zone. Arrows on X axis indicate transition between fresh, bloat, decay and post-decay stages. Vertical line indicates date of migration of oldest calliphorid prepupal larvae. See Table 2 for dates of day zero.

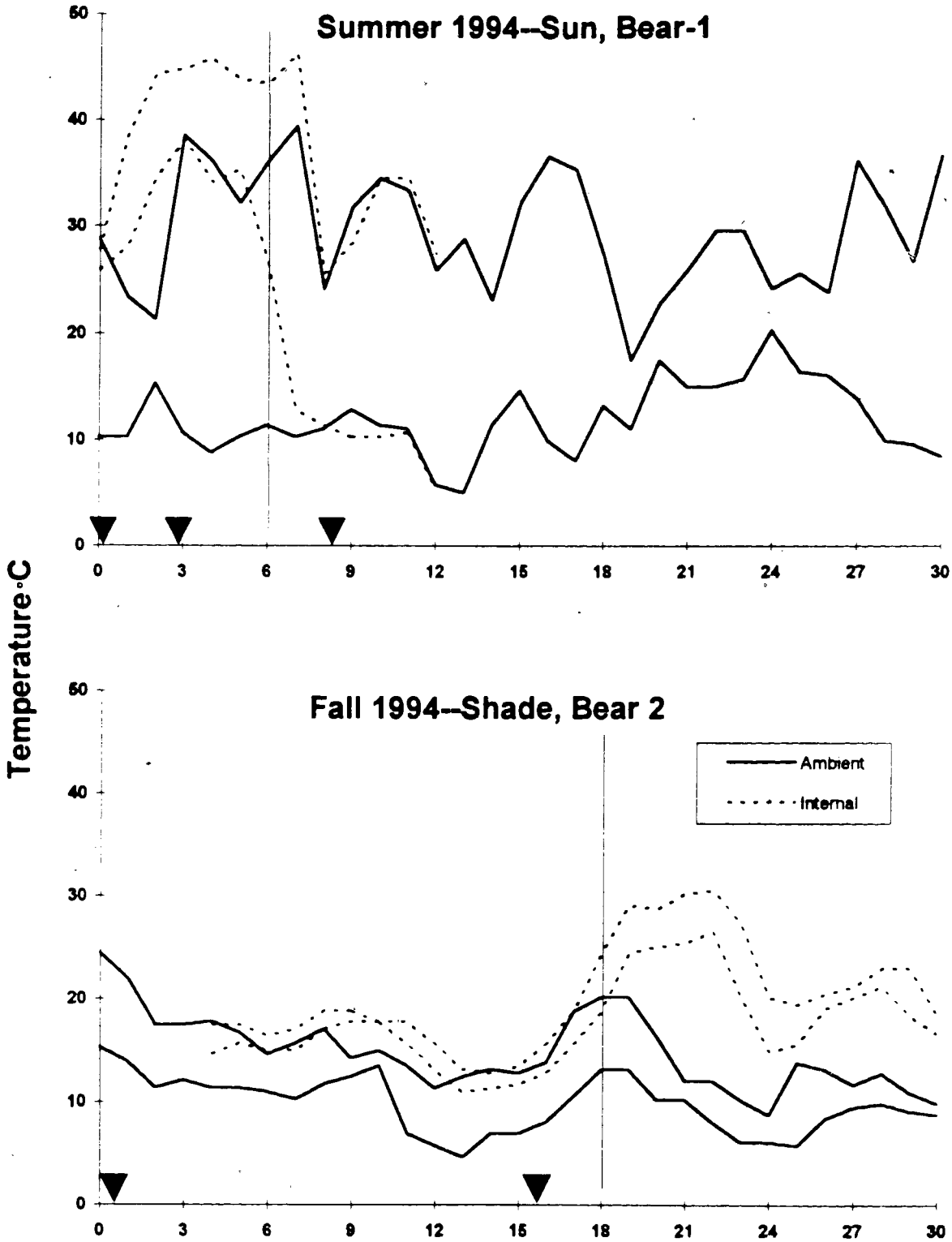

Summer 1994--Sun, Bear-1
Fall 1994--Shade, Bear 2
Ambient
Internal
Temperature°C
Days Since Death
0
10
20
30
40
50
0
3
6
9
12
15
18
21
24
27
30

Table 6. Summary of insects on 72 pig carcasses from May 1994 to June 1996, in three biogeoclimatic zones.

OBSERVATIONS	ZONES* CWH	IDF	SBS
Lucilia illustris co-dominant on carrion	YES	NO	NO
Phormia regina co-dominant on carrion	YES	YES	YES
Protophormia terraenovae co-dominant on carrion	NO	YES	YES
Calliphora vomitoria co-dominant on carrion, shade only	YES	NO	NO
Blow fly communities specific to habitat	YES	NO	NO
Blow fly communities specific to season	YES	NO	NO
Reduced insect numbers and diversity associated with desiccation, summer only	YES	NO	NO
Reduced insect numbers and diversity associated with cold temperatures	YES	YES	YES
Reduced insect succession after vertebrate scavenging	YES	N/A	YES
Clothing retained body fluids, apparently prolonging attraction to carcasses	YES	YES	YES
Insects found under clothing	YES	YES	YES
Clothed carcasses had a greater taxonomic diversity of insects than unclothed carcasses	YES	N/A	N/A

* YES = Observed. NO = Not observed. N/A = Not applicable—not included in research design.

Table 7. Summary of insects on seven wildlife carcasses, May 1994 to June 1996.

OBSERVATIONS	CARRION OBSERVED*			
	Bear 1	Bear 2	Cougars 1-3	Cougars 4,5
Lucilia illustris co-dominant on carrion	YES	NO	NO	NO
Phormia regina co-dominant on carrion	YES	YES	YES	NO
Protophormia terraenovae co-dominant on carrion	NO	NO	YES	NO
Calliphora vomitoria co-dominant on carrion	NO	YES	NO	NO
Blow fly communities consistent with those on pig carcasses in identical habitats, seasons, and zones	YES	YES	YES	N/A
Reduced insect numbers and diversity associated with cold temperatures	YES	YES	N/A	YES
Reduced insect succession after vertebrate scavenging	N/A	N/A	N/A	YES

*YES = Observed. NO = Not observed. N/A = Not applicable--not included in research design.

Table 8. Adult (A), immature (I), or both (B) insects collected from pig carrion during spring, summer and fall of 1994 in the CWH biogeoclimatic zone. Symbols for decomposition stages are: fresh (F), bloat (B), decay (D), post-decay (P), and remains (R).

SEASON	ORDER AND FAMILY	INSECT SPECIMENS	SUN UNCLOTHED F	B	D	P	R	SUN CLOTHED F	B	D	P	R	SHADE UNCLOTHED F	B	D	P	R
SPRING	COLEOPTERA																
	Histeridae	species undetermined				A		-	-	-	-	-					
	Hydrophilidae	*Megasternum posticatum* (Mannerheim)			A	A	A	-	-	-	-	-		A	A		A
		Sphaeridium lunatum G.				A		-	-	-	-	-					
	Leiodidae	*Catops basilaris* Say		A		A		-	-	-	-	-		A	A		A
	Nitidulidae	*Carpophilus* sp.					I	-	-	-	-	-					I
	Ptiliidae	*Acrotrichis* sp.						-	-	-	-	-	A	A			
	Silphidae	*Nicrophorus* sp.						-	-	-	-	-		A	A		
		Thanatophilus lapponicas (Herbst)		A				-	-	-	-	-					A
	Staphylinidae	*Creophilus maxillosus* (L.)		A	A	A		-	-	-	-	-		A	A		
		Ontholestes cingulatus (Grav.)			A			-	-	-	-	-					A
		Tribe Staphylinini	A	A	A	A	A	-	-	-	-	-	A	A	A	A	B
	Tenebrionidae	*Coniontis ovalis* LeConte						-	-	-	-	-					A
	DIPTERA							-	-	-	-	-					
	Calliphoridae	eggs	I					-	-	-	-	-	I	I			
		1st instars	I					-	-	-	-	-	I				
		2nd instars		I				-	-	-	-	-		I	I		
		3rd instars		I	I	I		-	-	-	-	-		I	I	I	
		prepupae		I	I			-	-	-	-	-			I		
		pupae			I	I		-	-	-	-	-			I		
		newly eclosed			A	A		-	-	-	-	-				A	A
		Calliphora sp.						-	-	-	-	-	A				
		Calliphora terraenovae Macquart	A					-	-	-	-	-	A	A			
		Calliphora vomitoria (L.)		A	A			-	-	-	-	-	B	B	B	B	
		Eucalliphora latrifrons (Hough)	A	A	B	B		-	-	-	-	-	B	B	B	B	
		Lucilia illustris (Meigen)		B	B	B		-	-	-	-	-	B	B	B	B	
		Phormia regina (Meigen)		B	I	B	A	-	-	-	-	-		A	A	A	A
	Ceratopogonidae	species undetermined				A		-	-	-	-	-					

SEASON	ORDER AND FAMILY	INSECT SPECIMENS	SUN UNCLOTHED F	B	D	P	R	SUN CLOTHED F	B	D	P	R	SHADE UNCLOTHED F	B	D	P	R
SPRING	Empidodae	species undetermined		A				-	-	-	-	-	A				
	Fanniidae	species undetermined						-	-	-	-	-					I
	Muscidae	species undetermined					A	-	-	-	-	-					A
	Phoridae	species undetermined	A	B	B	B		-	-	-	-	-	A	B	B	I	A
	Piophilidae	species undetermined		A		B	A	-	-	-	-	-		A	A		I
	Scathophagidae	species undetermined		A				-	-	-	-	-	A	A	A		A
	Sciaridae	species undetermined						-	-	-	-	-					A
	Sphaeroceridae	species undetermined			A		A	-	-	-	-	-		A			A
	Trichoceridae	species undetermined					A	-	-	-	-	-		A			A
	HYMENOPTERA							-	-	-	-	-					
	Braconidae	species undetermined						-	-	-	-	-		A	A		A
	Eucoilidae	*Kleidotoma* sp.					A	-	-	-	-	-					A
	Pteromalidae	*Nasonia vitripennis* (Walker)	A	A		A	B	-	-	-	-	-	A	A		A	A
SUMMER	**COLEOPTERA**																
	Agyrtidae	*Necrophilus hydrophiloides* Guérin-Méneville				A	A	-	-	-	-	-					A
	Erotylidae	*Deinopteroloma subcostatum* Mäkin			A			-	-	-	-	-					
	Hydrophilidae	*Megasternum posticatum* (Mannerheim)				A		-	-	-	-	-		A		A	
	Leiodidae	*Catops basilaris* Say				A		-	-	-	-	-					
		Catoptrichus frankenhaeuseri (Mannerheim)						-	-	-	-	-				A	
	Nitidulidae	*Carpophilus* sp.			I	I		-	-	-	-	-					
	Ptiliidae	*Acrotrichis* sp.				A		-	-	-	-	-				A	
	Scarabaeidae	*Onthophagus nuchicornis* (L.)						-	-	-	-	-				A	
	Silphidae	larval species undetermined				I		-	-	-	-	-					
	Staphylinidae	*Creophilus maxillosus* (L.)			A	A		-	-	-	-	-				A	
		Ontholestes cingulatus (Grav.)						-	-	-	-	-				A	
		Tribe Staphylinini	A		B	B	A	-	-	-	-	-	A	B		B	A
	DIPTERA																
	Calliphoridae	eggs	I	I				-	-	-	-	-	I	I			
		1st instars	I	I				-	-	-	-	-	I	I			
		2nd instars		I	I			-	-	-	-	-		I	I		
		3rd instars		I	I	I		-	-	-	-	-		I	I	I	

SEASON	ORDER AND FAMILY	INSECT SPECIMENS	SUN UNCLOTHED F	B	D	P	R	SUN CLOTHED F	B	D	P	R	SHADE UNCLOTHED F	B	D	P	R
SUMMER	Calliphoridae	prepupae			I	I		-	-	-	-	-		I	I	I	
		pupae				I		-	-	-	-	-			I	I	
		newly eclosed				A		-	-	-	-	-				A	
		Calliphora sp.	A			A		-	-	-	-	-	A	B		A	
		Calliphora terraenovae Macquart						-	-	-	-	-				A	
		Calliphora vomitoria (L.)						-	-	-	-	-		B	I	B	
		Eucalliphora latrifrons (Hough)	A	A		A		-	-	-	-	-	A	B		B	
		Lucilia illustris (Meigen)	A	B	I	A		-	-	-	-	-	B	B	B	B	
		Phormia regina (Meigen)	B	B	B	B		-	-	-	-	-		B	B	B	
		Protophormia terraenovae (R.-D.)	A	B	I	B		-	-	-	-	-					
	Dolichopodidae	species undetermined				A		-	-	-	-	-				A	
	Empidodae	species undetermined						-	-	-	-	-				A	
	Fanniidae	species undetermined				B		-	-	-	-	-				B	
	Muscidae	species undetermined				A		-	-	-	-	-		A	A	A	
	Phoridae	species undetermined				A	A	-	-	-	-	-		I		A	
	Piophilidae	species undetermined		A		B	I	-	-	-	-	-				B	
	Sarcophagidae	species undetermined				A		-	-	-	-	-			I		
	Scathophagidae	species undetermined				A		-	-	-	-	-				A	
	Sciaridae	species undetermined				A		-	-	-	-	-					
	Sphaeroceridae	species undetermined		A	A			-	-	-	-	-					
	Trichoceridae	species undetermined					A	-	-	-	-	-				A	
	HYMENOPTERA							-	-	-	-	-					
	Braconidae	species undetermined				A		-	-	-	-	-				A	
	Eucoilidae	*Kleidotoma* sp.				A		-	-	-	-	-				A	
	Pteromalidae	*Nasonia vitripennis* (Walker)				B		-	-	-	-	-				A	
FALL	**COLEOPTERA**																
	Agyrtidae	*Necrophilus hydrophiloides* Guérin-Méneville									A			A			
	Leiodidae	*Catops basilaris* Say									A	A		A	A		
	Nitidulidae	*Omosita inversa* LeConte										A					
	Ptiliidae	*Acrotrichis* sp.												A			
	Silphidae	*Nicrophorus* sp.												A			
	Staphylinidae	*Creophilus maxillosus* (L.)							A	A							

SEASON	ORDER AND FAMILY	INSECT SPECIMENS	SUN UNCLOTHED F	B	D	P	R	CLOTHED F	B	D	P	R	SHADE UNCLOTHED F	B	D	P	R
FALL	Staphylinidae	Tribe Staphylinini			B					A	A	A	A	B	A	A	
	DIPTERA																
	Calliphoridae	eggs	I					I					I				
		1st instars	I	I				I	I				I				
		2nd instars	I	I	I	I		I	I	I			I	I			
		3rd instars		I	I	I			I	I	I			I	I	I	
		prepupae			I	I				I	I				I	I	
		pupae				I				I	I				I		
		newly eclosed									A						
		Calliphora sp.		A	A			A	B				A	B			
		Calliphora vomitoria (L.)		B	B			A	B	B			A	B	B	A	
		Lucilia illustris (Meigen)		B										A	A		
		Phormia regina (Meigen)							B	B				A			
	Drosphilidae	species undetermined			I	I					I						
	Empidodae	species undetermined				A							A	A			
	Fanniidae	species undetermined									A	A					
	Heleomyzidae	species undetermined							A					A			
	Muscidae	species undetermined		A				A	A	A			A	A			
	Phoridae	species undetermined												A			
	Piophilidae	species undetermined									A	B		A			
	Scathophagidae	species undetermined				A			A				A	A	A		
	Sciaridae	species undetermined												A			
	Sphaeroceridae	species undetermined										A					
	Trichoceridae	species undetermined		A								A		A			
	HYMENOPTERA																
	Braconidae	species undetermined			A	A					A						
	Pteromalidae	*Nasonia vitripennis* (Walker)		A		A								A			

Table 9. **Adult (A), immature (I), or both (B) insects collected from clothed pig carrion during spring and summer of 1994 in the IDF biogeoclimatic zone. Symbols for decomposition stages are: fresh (F), bloat (B), decay (D), post-decay (P), and remains (R).**

SEASON	ORDER AND FAMILY	INSECT SPECIMENS	SUN					SHADE				
			F	B	D	P	R	F	B	D	P	R
SPRING	COLEOPTERA											
	Cleridae	*Necrobia rufipes* (DeG.)			A	A			A			
		Necrobia violacea (L.)				A			A		A	
	Dermestidae	*Apsectus* sp.			I	I					I	
		Dermestes marmoratus Say			A					A		
		Dermestes talpinus Mannerheim		A	A	A			A	A	B	
	Histeridae	species undetermined			A	A					A	
	Hydrophilidae	*Sphaeridium lunatum* G.							A		A	
	Nitidulidae	*Carpophilus* sp.				I						
		Omosita inversa LeConte		A	A	A			A			
	Scarabaeidae	*Onthophagus nuchicornis* (L.)		A		A					A	
	Silphidae	*Heterosilpha ramosa* (Say)									A	
		larval species undetermined			I	I					I	
		Necrodes surinamensis (F.)								A	A	
		Nicrophorus sp.		A		A			A	A	A	
		Thanatophilus lapponicas (Herbst)		A	A	A			A		A	
	Staphylinidae	*Creophilus maxillosus* (L.)		A	A	B			A	A	B	
		Ontholestes cingulatus (Grav.)				A			A		A	
		Tribe Staphylinini				B			A			
	DIPTERA											
	Calliphoridae	eggs	I	I				I	I			
		1st instars		I				I	I			
		2nd instars		I					I	I	I	
		3rd instars		I	I	I			I	I	I	
		prepupae			I	I				I	I	
		pupae			I	I				I	I	
		newly eclosed				A					A	
		Calliphora sp.				A					A	
		Calliphora vomitoria (L.)		A					B		A	

SEASON	ORDER	INSECT SPECIMENS	SUN					SHADE				
			F	B	D	P	R	F	B	D	P	R
SPRING	Calliphoridae	*Eucalliphora latrifrons* (Hough)		A								
		Lucilia illustris (Meigen)				A			B		B	
		Phormia regina (Meigen)		B	B	B			B	B	B	
		Protophormia terraenovae (R.-D.)		B	B	B			B	B	B	
	Fanniidae	species undetermined				A					A	
	Muscidae	species undetermined							A			
	Phoridae	species undetermined			A	A					A	
	Piophilidae	species undetermined				A					B	
	Sarcophagidae	species undetermined									A	
	Sciaridae	species undetermined		A								
	Sphaeroceridae	species undetermined				A						
	Trichoceridae	species undetermined							A			
	HYMENOPTERA											
	Braconidae	species undetermined				A						
	Eucoilidae	*Kleidotoma* sp.				A						
SUMMER	**COLEOPTERA**											
	Cleridae	*Necrobia violacea* (L.)				A					A	
	Dermestidae	*Apseotus* sp.			I	I			I			
		Dermestes talpinus Mannerheim		A	B	B			B	A	A	
	Histeridae	species undetermined			A	A			A	A	B	
	Leiodidae	*Sciodrepoides fumatus terminans* (LeConte)				A						
		Catops basilaris Say				A					A	
	Nitidulidae	*Carpophilus* sp.				I						
		Omosita inversa LeConte				A					A	
	Scarabaeidae	*Onthophagus nuchicornis* (L.)			A				A			
	Silphidae	larval species undetermined				I						
		Necrodes surinamensis (F.)			A				A	A		
		Nicrophorus sp.			A	A			A	A	A	
		Thanatophilus lapponicas (Herbst)		A	A	A				A	A	
	Staphylinidae	*Creophilus maxillosus* (L.)			A	B			A	A	B	
		Ontholestes cingulatus (Grav.)			A				A			
		Tribe Staphylinini				A	A		B			A

SEASON	ORDER	INSECT SPECIMENS	SUN					SHADE				
			F	B	D	P	R	F	B	D	P	R
SUMMER	**DIPTERA**											
	Calliphoridae	eggs	I	I				I	I			
		1st instars		I				I	I			
		2nd instars		I	I			I	I			
		3rd instars		I	I	I			I	I	I	
		prepupae			I	I			I	I	I	
		pupae				I				I	I	
		newly eclosed				A						
		Calliphora vomitoria (L.)				A						
		Phormia regina (Meigen)		B	B	B			B	B	B	
		Protophormia terraenovae (R.-D.)							B	B	B	
	Fanniidae	species undetermined				B	B			B	B	
	Muscidae	species undetermined							A			
	Piophilidae	species undetermined			A	B	B		A	B	B	B
	Sarcophagidae	species undetermined							B	B	B	
	Scathophagidae	species undetermined				A					A	
	Sciaridae	species undetermined								A	A	
	Sphaeroceridae	species undetermined				A	A				A	
	HYMENOPTERA											
	Braconidae	species undetermined									A	
	Ichneumonidae	species undetermined			A							

Table 10. Adult (A), immature (I), or both (B) insects collected from clothed pig carrion during spring and summer of 1994 in the SBS biogeoclimatic zone. Symbols for decomposition stages are: fresh (F), bloat (B), decay (D), post-decay (P), and remains (R).

SEASON	ORDER AND FAMILY	INSECT SPECIMENS	SUN					SHADE				
			F	B	D	P	R	F	B	D	P	R
SPRING	COLEOPTERA											
	Cleridae	*Necrobia rufipes* (DeG.)			A	A			A			
		Necrobia violacea (L.)			A	A			A			
	Dermestidae	*Apsectus* sp.				I				I	I	
		Dermestes talpinus Mannerheim		A	A	B			A	B	B	
	Histeridae	species undetermined		A	A	B			A	A	B	
		Saprinus lugens Erichson								A		
	Hydrophilidae	*Megasternum posticatum* (Mannerheim)									A	
		Sphaeridium lunatum G.			A				A			
	Lathridiidae	*Cortinicara gibbosa* (Herbst)							A			
	Leiodidae	*Catops basilaris* Say							A		A	
	Nitidulidae	*Carpophilus* sp.								I		
	Scarabaeidae	*Onthophagus nuchicornis* (L.)			A	A			A			
	Silphidae	*Heterosilpha ramosa* (Say)			A	A						
		larval species undetermined			I	I				I	I	
		Necrodes surinamensis (F.)									A	
		Nicrophorus defodiens Mannerheim							A			
		Nicrophorus sp.		A	A	A			A	A	A	
		Thanatophilus lapponicas (Herbst)			A	A				A	A	
	Staphylinidae	*Creophilus maxillosus* (L.)			A	B			A	A	B	
		Ontholestes cingulatus (Grav.)		A	A	A			A	A	A	
		Tribe Staphylinini			A	B			A		A	
	Calliphoridae	eggs	I	I				I	I			
		1st instars		I					I			
		2nd instars		I					I			
		3rd instars		I	I	I			I	I	I	
		prepupae		I	I	I				I	I	

SEASON	ORDER AND FAMILY	INSECT SPECIMENS	SUN					SHADE				
			F	B	D	P	R	F	B	D	P	R
SPRING	Calliphoridae	pupae			I	I				I	I	
		newly eclosed				A					A	
		Calliphora sp.								B		
		Calliphora vomitoria (L.)			A	A				A	A	
		Lucilia illustris (Meigen)			A						I	
		Phormia regina (Meigen)		B	B	B			B	B	B	
		Protophormia terraenovae (R.-D.)		B	B	B			B	B	B	
	Dilichopodidae	species undetermined									A	
	Drosophilidae	species undetermined									A	
	Fanniidae	species undetermined				B				A	B	
	Muscidae	species undetermined			A	A					A	
	Phoridae	species undetermined				A					A	
	Piophilidae	species undetermined			A	B				A	A	
	Sarcophagidae	species undetermined			B	B				B	B	
	Scathophagidae	species undetermined			A					A		
	Sphaeroceridae	species undetermined				A					A	
	HYMENOPTERA											
	Braconidae	species undetermined				A	A					
SUMMER	**COLEOPTERA**											
	Dermestidae	*Apsectus* sp.				I						
		Dermestes talpinus Mannerheim				B					A	
	Histeridae	species undetermined			A	A				A	A	
	Hydrophilidae	*Sphaeridium lunatum* G.				A						
	Leiodidae	*Catops basilaris* Say								A		
	Nitidulidae	*Omosita inversa* LeConte				A						
	Silphidae	*Heterosilpha ramosa* (Say)			A							
		larval species undetermined			I	I					I	
		Necrodes surinamensis (F.)			A				A	A		
		Nicrophorus defodiens Mannerheim		A								
		Nicrophorus investigator Zetterstedt		A					A			
		Nicrophorus sp.			A	A		A	A	A	A	
		Nicrophorus vespillodes Herbst		A								

SEASON	ORDER AND FAMILY	INSECT SPECIMENS	SUN					SHADE				
			F	B	D	P	R	F	B	D	P	R
SUMMER	Silphidae	*Oiceoptoma noveboracense* (Forster)				A						
		Thanatophilus lapponicas (Herbst)		A	A	A			A	A		
	Staphylinidae	*Creophilus maxillosus* (L.)			A	B	A		A	A	B	
		Ontholestes cingulatus (Grav.)							A			
		Tribe Staphylinini				A	A			A	A	
	DIPTERA											
	Calliphoridae	Diptera eggs	I	I				I	I			
		1st instars		I				I	I			
		2nd instars		I	I			I	I			
		3rd instars		I	I	I			I	I	I	
		prepupae			I	I				I	I	
		pupae				I				I	I	
		newly eclosed				A					A	
		Calliphora sp.			A				A			
		Calliphora vomitoria (L.)			A							
		Lucilia illustris (Meigen)			A							
		Phormia regina (Meigen)		B	B	B			B	B	B	
		Protophormia terraenovae (R.-D.)		B	B	B			B	B	B	
	Fanniidae	species undetermined			A	B	B			A	B	
	Muscidae	species undetermined			A	A			A	A	A	
	Phoridae	species undetermined				A				A	A	
	Piophilidae	species undetermined			A	B	B		A	B	B	
	Sarcophagidae	species undetermined			B	B						
	Scathophagidae	species undetermined							A		A	
	Sepsidae	species undetermined				A						
	Sphaeroceridae	species undetermined			A						A	
	HYMENOPTERA											
	Braconidae	species undetermined								A		

Table 11. Checklist of insect species associated with wildlife carrion.

ORDER AND FAMILY	INSECT SPECIMENS	SUMMER SUN Bear 1	FALL SHADE Bear 2	SUMMER SUN Cougars 1-3	WINTER SHADE Cougars 4,5
COLEOPTERA					
Agyrtidae	*Necrophilus hydrophiloides* Guérin-Méneville	X	X		
Erotylidae	*Deinopteroloma subcostatum* Mäkin		X		
Histeridae	larval species undetermined			X	
	species undetermined			X	
Leiodidae	*Catops basilaris* Say	X			X
	Catoptrichus frankenhaeuseri (Mannerheim)	X	X		X
Nitidulidae	*Carpophilus* sp.		X		
Silphidae	larval species undetermined			X	
	Necrodes surinamensis (F.)			X	
	Nicrophorus sp.			X	
Staphylinidae	Tribe Athetini				X
	Creophilus maxillosus (L.)	X		X	
	Omalium foraminosum Mäkin	X			
	Tribe Staphylinini	X			X
DIPTERA					
Anthomyiidae	species undetermined	X			
Calliphoridae	*Calliphora vomitoria* (L.)	X	X		
	Lucilia illustris (Meigen)	X			
	Phormia regina (Meigen)	X	X	X	
	Protophormia terraenovae (R.-D.)			X	
Fanniidae	larval species undetermined	X	X	X	
	species undetermined	X			
Muscidae	species undetermined	X	X		
Phoridae	species undetermined	X	X		
Piophilidae	larval species undetermined	X		X	
	adult species undetermined	X		X	
Scathophagidae	species undetermined	X			
Trichoceridae	species undetermined		X		X
HYMENOPTERA					
Braconidae	species undetermined		X		
Ichneumonidae	species undetermined		X		

4. DISCUSSION

My results add substantially to the knowledge of the biology and forensic importance of carrion-feeding insects in B.C. Of particular significance are: the role of habitat and season on rate of decomposition and blow fly activity; the influence of clothing and scavenging on carrion fauna and hence the speed of decomposition; the early arrival on carrion of insects previously considered to occur in late successional stages; and pertinent differences on wildlife carcasses in the biology and role of decomposition caused by carrion-feeding insects.

In retrospect, the role of clothing on carrion-feeding insects and attendent rate of decomposition would have been elucidated more clearly had a well-replicated experiment been designed that compared decomposition of clothed *versus* unclothed carcasses during the same time frame within a single biogeoclimatic zone. Furthermore, a reliable comparison between the CWH and the other two zones, IDF and SBS, was not possible because all carcasses in the IDF and SBS zones were clothed, whereas observations were made only on two clothed carcasses in the CWH zone.

4.1 Effects of Habitat and Season

My data showed that habitat (sun and shade) and season (spring, summer and fall) influenced the rate of decomposition (Figures 6 and 7). High temperatures contributed to fast decay whereas cold temperatures prolonged decay. In the CWH zone, the time for 50% carrion weight reduction to occur ranged from six days in the sun during summer to 60 days in the shade during fall (Figure 6). The rate of decomposition has been determined in several carrion ecology experiments by measuring loss of carcass weight over time (Anderson & VanLaerhoven 1996; Shean *et al.* 1993; Hewadikaram & Goff 1991; Payne 1965). Loss of carcass weight has been attributed to dipteran feeding activity (Denno & Cothran 1975), maggot migration, and dehydration (Shean *et al.* 1993). In agreement with the literature, and despite short-term increases in weight due to absorption of moisture, weight loss of unclothed carcasses in my study was a representative measure of decomposition.

Habitat and season did not appear to influence the types of blow flies found on carcasses. Although numbers of some blow fly species varied by habitat, species previously reported to be associated with sun (*Lucilia illustris*) or shade (*Calliphora vomitoria*) habitats (Smith 1986) were found in both habitats (Tables 8-11). Hence, neither species can be considered as specific indicators of habitat type. The drive to oviposit may lead *Lucilia* sp. to

be found in the shade (Greenberg 1988), and similarly may cause *C. vomitoria* to be found in the sun. *Calliphora vomitoria*, *Phormia regina* and *Protophormia terraenovae* are reported to be most common during cool seasons in North America (Smith 1986), but I found little seasonal preference. Denno & Cothran (1975) suggest that *P. regina* uses carcass size as a means of resource partitioning. However, *P. regina* was found on both 22 kg (50 lb.) pig and 90 kg (200 lb.) bear carcasses, suggesting that if resource partitioning occurs it may occur below or above this weight range. Because *P. terraenovae* is reportedly most common at high elevations (Smith 1986) and both IDF and SBS zones are at high elevations (~738 m and 676 m respectively) at the latitude of the test sites, elevation may be a greater influence on the presence of *P. terraenovae* than season or habitat. Blow flies *L. illustris* and *C. vomitoria* may also have biogeoclimatic preferences (Tables 8-11). As confirmed by case work conducted in B.C. (Anderson 1995), *L. illustris* and *C. vomitoria* may be most characteristic of the CWH zone, and *P. terraenovae* of the IDF and SBS zones.

Habitat and season influenced blow fly activity on carcasses. Typically, the warmer the temperature of a habitat or season, the faster the development of blow flies (Smith 1986). Overnight temperatures < 0°C may have caused a delay in calliphorid egg-laying on carcasses during spring in both the IDF and the SBS zones and a subsequent delay in development (Table 3, Figures 10 and 11). Immediate oviposition can not be assumed for these zones during spring, and this finding must be considered, together with weather records, in the forensic use of blow fly oviposition to indicate time since death.

Peak internal temperatures may play a lesser role in blow fly larval development than previously reported because my research indicated that calliphorid larval migration usually began before peak internal temperatures were reached in sun and shade during spring, summer and fall. Recent studies suggest that internal temperatures could be used in addition to ambient temperatures to determine rates of blow fly development (Catts & Goff 1992; Turner & Howard 1992; Greenberg 1990). However, the use of peak internal temperatures may be misleading in estimating larval age, thus lessening the value of this measure for forensic investigations.

Internal carcass temperatures may not accurately represent the temperatures at which all maggots on the carcass live. Probing different depths of a single maggot mass as well as different masses located within the same carcass produced differences in temperature readings as large as 10°C (Figure 12). Maggots do not live continuously at maximum internal temperatures, but rather live at several degrees cooler than maximum, because they continuously move in and out of a

mass while feeding (Anderson & VanLaerhoven 1996; Dillon & Anderson 1995) and move to different feeding areas on the same carcass. Forensic investigators using hand-held thermometers may overestimate thermal histories of larval aggregations. Overestimations are problematic because they may be used to determine time of death in forensic investigations (Anderson & VanLaerhoven 1996). Future research examining the thermal histories of individual maggots within a mass is thus needed (Anderson & VanLaerhoven 1996; Dillon & Anderson 1995; Greenberg 1991).

In habitats and seasons with high ambient temperatures, movement of maggots away from carcasses was apparently linked to the need for more food resources rather than stage of development. If such movement is misinterpreted to be the prepupal wandering stage, erroneous assumptions regarding time of death could be made. In addition, movement of objects, *e.g.* bullets, bones and clothing, by maggots may create postmortem artifacts in death investigations.

The presence of both undersized puparia and undersized adult blow flies may be a symptom of high temperatures and exposed habitats. Laboratory studies have indicated that there is high mortality when severe larval competition occurs; in addition both pupae and newly eclosed flies may be under-sized, and no peak in emergence may occur (Smith 1986; Denno & Cothran 1975; Kamal 1958). Although larval mortality from insufficient food is difficult to measure in field situations, high densities of larvae occurred on carrion placed in sun, during summer. In the CWH zone, puparia and eclosing flies were notably small in size. This observation may help in identifying the season and habitat in which death occurred. Unlike laboratory studies (Smith 1986; Denno & Cothran 1975; Kamal 1958), a peak in emergence was observed in the field. This difference may be attributed to the size of carrion used. Laboratory carrion samples may have been too small to generate sufficient numbers of flies to provide data which could indicate peak emergence.

Insufficient food did not alter the rate of blow fly development for various species in the laboratory (Anderson 1997). Hence, current developmental data based on adequate food resources may be useful in determining larval age in high larval competition situations. However, larval competition makes identifying the most advanced stage of maggot development difficult. Where there was less competition, distinct masses of maggots of the same age co-inhabited the carcasses. In fierce competition, maggots were less uniform in size. In such cases old, yet undersized, larvae may be present but obscured by the presence of younger maggots of normal size. Forensic investigators are advised to collect the "largest larvae (*sic.*) specimens observed...since they represent the earliest insect in successional pattern" (Rodriguez & Bass

1983). This instruction could lead to inaccurate estimates of blow fly larval age. As well, Rodriguez and Bass (1983) ignore other dipteran larval forms in families such as Fanniidae and Piophilidae, which have characteristically small larvae that occur later in the successional pattern than most calliphorid larvae.

4.2 Influence of Clothing

Clothing masks the expression of typical decay stages. Misinterpretation of decompositional stage may lead to incorrect categorization of the decomposition process, leading in turn to erroneous estimates of elapsed time since death. In addition, most researchers classify carrion into decompositional stages to present successional data on animal models, compounding possible errors. My attempts to search for evidence of discrete stages were limited because I wanted to minimize disturbances to carcasses and insect activity. A change in the research design to measure bloat by girth measurements (Shean *et al.* 1993) in addition to visual observations may have provided more quantitative evidence.

Although weight of clothed carcasses declined with days since death (Figures 6 and 7), the decline was sporadic, apparently because clothing absorbed body fluids and rain, and prepupal maggots predominately pupated in the clothing rather than in the soil. Maggot migration from the carcass, partially responsible for weight loss (Shean *et al.* 1993), was not observed, and hence weight loss was not a representative measure of decomposition rate of clothed carcasses.

Several authors infer that clothing affects the rate of decomposition (Haglund 1991; Mann *et al.* 1990; Rodriguez & Bass 1983). Their studies are not supported by experimental research. Moreover, they present conflicting opinions as to whether clothing retards (Haglund 1991) or enhances (Mann *et al.* 1990; Rodriguez & Bass 1983) decomposition. My data indicate that clothing increases the rate of decomposition (Figure 4), probably because of increased insect infestation as a result of more ovipositional sites, and emerging larvae.

Blow flies selectively oviposit (Kamal 1958) where exuding fluids such as blood, muscle plasma and body fluids occur because eggs are susceptible to desiccation and early stages of calliphorid larvae require fluids to feed on (Smith 1986). Fluid-soaked clothing apparently provided more ovipositional substrate than that found on unclothed carcasses, resulting in more eggs, greater hatching success, larger larval aggregations, and hence increased decomposition compared with unclothed carcasses (Figure 4).

Although, high densities of blow fly larvae also occurred on clothed carcasses in the IDF and SBS zones, there were no undersized puparia or adult flies, typical of high larval competition (Smith 1986; Denno & Cothran 1975; Kamal 1958). Additional shelter for beetles predating on larvae was created by clothing and predator activity may have reduced competition between blow fly larvae. Thus, in these biogeoclimatic zones the presence of undersized puparia and adult blow flies may be more indicative of unclothed carrion. Because clothing may disintegrate before a forensic investigation begins, the size of empty pupal cases may provide important clues.

Clothing increased numbers and diversity of successional insects (Table 8). Moist clothing seemed to be very attractive to piophilids and fanniids, possibly because moist food is required prior to oviposition (Simmons 1927), and semi-liquid conditions are required for optimal development (Smith 1986). In addition, clothing provided shelter from sunlight, and may have created attractive conditions for calliphorid, piophilid and fanniid larvae because they exhibit a strong negative phototaxis (Kamal 1958; Hall 1948; Simmons 1927). Clothing sheltered both diurnal and nocturnal insect species because both types of insects were found within folds of clothing during the day, facilitating their collection. Large and diverse insect populations may thus be expected within clothing on carcasses, and forensic investigators should scrutinize clothed and unclothed cadavers when seeking entomological evidence.

4.3 Influence of Scavenging

Scavenging decreased the duration or eliminated decompositional stages in pig and wildlife carcasses, thus reducing numbers of insects that arrive later and creating postmortem artifacts. Although weight reduction of scavenged carcasses in shade resembled that of unscavenged carcasses in sun, weight loss was primarily through scavenging, and does not provide a representative measure of decomposition.

Vertebrate scavengers removed clothing, and soft tissue of pig carcasses eliminating potential food for late-arriving successional insects. In non-scavenged carcasses, calliphorid activity is followed by a wave of successional insects such as other species of flies, and skin beetles (Smith 1986), that will feed on soft tissue of the carcass not consumed by blow fly maggots. Scavengers create difficulties in establishing time of death by means of forensic entomology. Insect species, common in late decay stages, may not have had sufficient food and as a result may not be found associated with scavenged carcasses.

Scavenging varied by season. No scavenging on carcasses was observed during summer experiments possibly because the speed of soft tissue removal by insects as well as the speed of

decomposition were more intense and limited the time available for scavenging. In cooler seasons, blow fly activity and decomposition proceed at a slower rate, which would allow more time for scavenging. These findings concur with observations by forensic investigators who found that completely articulated skeletons are typical of deaths in summer, whereas intense scavenged remains are typical of deaths in winter (Newell 1996; Stair 1995). However, Mann (1990) interprets a lack of scavenging during hot weather to be an indication that the body has been moved to the site of discovery. An additional hypothesis is that facultative scavengers have more alternative sources of food available to them in summer.

Scavenging alters host carrion by creating post-mortem artifacts such as enlarged wound sites, bite marks and tissue removal. Scavenging in the CWH zone was commonly initiated at bullet wounds and enlarged them. Calliphorid flies are attracted to wounds for oviposition. Enlarged wounds can accommodate larger numbers of blow fly eggs than small ones, resulting in larger maggot masses, which speed decomposition. Such post-mortem alteration of soft-tissue has received minimal attention in forensic literature (Haglund 1992), indicating a need for more research.

4.4 Succession

Arrival times of important successional insects occurred earlier than suggested in national (Johnston & Villeneuve 1987) and international (Smith 1986; Erzinclioglu 1985; Nuorteva 1977; Easton & Smith 1970; Reed 1958; Mégnin 1894) literature. These findings confirm work conducted in similar temperate regions (Anderson & VanLaerhoven 1996; Anderson 1995; Shean 1993; Rodriguez & Bass 1983; Chapman & Sankey 1955). Although studies in North America and Europe indicate that members of the Piophilidae arrive on carrion three to six months after death (Smith 1986; Nuorteva 1977; Reed 1958; Johnston & Villeneuve 1897), in B.C. larval colonies of piophilids were found on clothed carcasses as early as three weeks after death (Tables 8-10). Early times of arrival were also observed for members of the families Cleridae [*Necrobia rufipes* (DeG.), *Necrobia violacea* (L.)], Dermestidae (*Aspectus* sp., *Dermestes marmoratus* Say, *Dermestes talpinus* Mannerheim), Fanniidae, Histeridae, Leiodidae [*Catops basillaris* Say, *Catoptrichus frankenhaeuseri* (Mannerheim), *Sciodrepoides fumatus terminans* (LeConte)], Nitidulidae (*Carpophilus* sp., *Omosita inversa* LeConte), Silphidae [*Heterosilpha ramosa* (Say), *Necrodes surinamensis* (F.), *Nicrophorus defodiens* Mannerheim, *Nicrophorus investigator* Zetterstedt, *Nicrophorus vespillodes* Herbst, *Oiceoptoma novaboracense* (Foster), *Thanatophilus lapponicas* (Herbst)], and Tenebrionidae (*Coniontis ovalis* LeConte) (Tables 8-

10). A single observation was made of a tenebrionid (*C. ovalis*) on pig carrion 10 months after death (Table 8), suggesting that tenebrionids may be associated with carrion approximately two years earlier in the CWH zone than expected in other regions of Canada (Johnston & Villeneuve 1897).

Colonization of many successional insects was influenced by season. In general, the warmer the season, the earlier the time of establishment for fanniids, dermestids, piophilids, staphylinids, and silphids (Tables 8-10). Forensic investigators must take season into consideration when determining time of death based on times of insect arrival. Although colonization times between habitats differed by zero to five days following death (earliest arrivals were usually found in the sun), habitat did not appear to influence the majority of successional insects (Tables 8-10). On carcasses that were scavenged, or subjected to cold temperatures, subsequent insect colonization was delayed or did not occur.

Some successional insects were characteristic of particular seasons. In particular, *Necrophilus hydrophiloides* Guérin-Méneville was characteristic of temperatures < 10°C. In the CWH zone, temperatures below this range usually occur from late September until late March (Meidinger & Pojar 1991). *Necrophilus hydrophiloides* provides entomological evidence of cool temperatures, which is when most other insects are inactive and not found.

Colonization times are also influenced by the presence or absence of moisture and this needs to be considered in time of death determinations. Reduced moisture discouraged some insects (piophilids and fanniids) but favored the presence of others (clerids and dermestids). Aggregations of piophilid larvae did not occur on desiccated carcasses until three months after death (Table 8), consistent with some European and North American literature (Smith 1986; Nuorteva 1977; Reed 1958; Johnston & Villeneuve 1897). Simmons (1927) states that piophilids require moist food for oviposition and that eggs laid on a dry surface fail to eclose. This may explain the delay or lack of piophilid colonization on desiccated carrion. In contrast, desiccated carrion favored the presence of clerids and dermestids. Typical wet climatic conditions of the CWH zone did not provide the dry conditions necessary for dermestid activity (Smith 1986; Howden 1950). As a result, dermestids showed a biogeoclimatic preference for dry zones–IDF and SBS–and may be of specific, but geographically limited, use in forensic investigations.

4.5 Wildlife

The longer post-decay stage in unscavenged wildlife carcasses than pig carcasses. (Figures 5) can be attributed to the amount of fur, and large mass (skin, bone, cartilage, and non-muscle tissue) that is still left to decompose during this stage. These results differ from those found in a tropical environment (Hewadikaram & Goff 1991), where a short post-decay stage was associated with a large carcass; however, they examined the effects of size in small pig carcasses only. Examining elephant carrion, Coe (1978) also found that the post-decay stage was short relative to the dry (remains) stage, but scavenging activity may have increased decomposition.

As in other studies (Mann *et al.* 1990; Johnson 1975), hair fell off wildlife carcasses in clumps during the decay stage. Thereafter, in Bears 1 and 2 (Figure 8), there was no weight increase due to absorbed moisture by animal hair. Thus, decomposition of wildlife carcasses could be measured based on weight because weight loss was attributed to maggot migration, hair loss, loss of moisture and maggots adhering to hair, and decomposition. Fur on wildlife carcasses did not impede blow fly oviposition near wound sites. These findings have utility for identification of wound sites in illegally killed wildlife.

In fresh wildlife carcasses, increased internal temperatures were observed before the formation of maggot masses (Figure 13). These temperatures corresponded with the maximum ambient temperatures recorded during the same period. Thick fur may have reduced internal heat loss. High internal temperatures during initial stages of larval development will shorten development rates of blow flies. Unlike findings with pig carcasses, internal temperatures in dark, furred wildlife may play an important role in larval development. Consequently, internal temperatures may be more reliable predictors of time since death in wildlife than in pigs and humans.

Wildlife carcasses of large size, 68-90 kg (150-200 lb.) for black bears; 36 kg (80 lb.) for adult cougars, contained large numbers of calliphorid larvae. Despite high densities of blow fly larvae, no competition, and undersized puparia or adult flies were not detected. Because food resources on large wildlife carcasses are apparently not limiting, the occurrence of migrating maggots probably indicates that they have reached the prepupal stage.

The diversity and times of arrival of insects attracted to clothed or furred carcasses were very similar, which may indicate that data obtained from clothed carcasses may be useful in wildlife poaching investigations. More research comparing wildlife carcasses with clothed carcasses is warranted.

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