SUCCESSIONAL BIODIVERSITY IN INSECT SPECIES ON BURIED CARRION IN THE VANCOUVER AND CARIBOO REGIONS OF BRITISH COLUMBIA

by

Sherah Lynnette VanLaerhoven

B.Sc. Simon Fraser University 1994

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF PEST MANAGEMENT
in the Department
of
Biological Sciences

SIMON FRASER UNIVERSITY

April 1997

National Library of Canada

Acquisitions and Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale du Canada

Acquisitions et services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

0-612-24261-7

APPROVAL

Name: Sherah Lynnette Van Laerhoven

Degree: Master of Pest Management

Title of Thesis:

SUCCESSIONAL BIODIVERSITY IN INSECT SPECIES ON BURIED CARRION IN THE VANCOUVER AND CARIBOO REGIONS OF BRITISH COLUMBIA

Examining Committee:

Chair: Dr. R. Brooke, Associate Professor

Dr. G. S. Anderson, Assistant Professor, Senior Supervisor
Department of Biological Sciences, SFU

Dr. J. H. Borden, Professor
Department of Biological Sciences, SFU

Dr. K. Lertzman, Associate Professor
School of Resource/Environmental Management, SFU

Staff Sgt. Robert Stair
Royal Canadian Mounted Police (Retired)

Dr. D. Gillespie, Research Scientist
Agriculture and Agri-Food Canada
Public Examiner

Date Approved: 14 April 1997

ABSTRACT

I established a database of insect succession on buried carrion in two biogeoclimatic zones of British Columbia over a 16 month period beginning June 1995. Pig (*Sus scrofa* L.) carcasses were buried immediately after death, buried 48 h after death, and buried then subsequently disturbed, in the Coastal Western Hemlock and Sub-boreal Spruce biogeoclimatic zones of British Columbia. Buried pigs exhibited a distinct pattern of insect diversity, relative abundance and succession from that which occurred on above-ground carrion. Insect communities on buried carrion exhibited greater species richness and evenness compared with above-ground carrion. The species composition and time of colonization for particular species differed between the two zones. Therefore ideally, a database of insect succession on buried carrion should be established for each major biogeoclimatic zone. I did not observe maggot masses on any of the buried carcasses, therefore the presence of maggot masses may indicate a delayed burial. Soil temperature was a better indicator of internal buried carcass temperature ($r^2=0.92$, $P<0.0001$) than was ambient air temperature ($r^2=0.60$, $P<0.0001$), thus soil temperature should be used to determine developmental rates of insects for determination of the post-mortem interval by a forensic entomologist.

To Gail, John and Dave -

for always believing in me.

Poor soul, the centre of my sinful earth,
these rebel powers that thee array;
Why dost thou pine within and suffer death,
Painting thy outward walls so costly gay?

Why so large cost, having so short a lease,
Dost thou upon thy fading mansion spend?
Shall worms, inheritors of this excess,
Eat up thy charge? is this thy body's end?

Then soul, live thou upon thy servant's loss,
And let that pine to aggravate thy store;
Buy terms divine in selling hours of dross;
Within be fed, without be rich no more:

So shalt thou feed on Death, that feeds on men,
And Death once dead, there's no more dying then.

William Shakespeare, Sonnet 146

ACKNOWLEDGEMENTS

This research was supported by the Canadian Police Research Centre, especially Sgt. Ken Beiko and Mr. Nick Cartwright. I would like to thank the Malcolm-Knapp Research Forest and the Alex Fraser Research Forest staff for their kind cooperation; all the high school and undergraduate volunteers, friends and collegues who spent many hours digging graves, placing carcasses, collecting pitfall traps and sorting through soil; G. St. Hilaire for his assistance placing carcasses; Anderson lab-mates for assistance throughout the research; Simon Fraser University for the use of its facilities; Dr. T. Finlayson, Dr. H.R. MacCarthy and the International Association for Identification for their generous scholarship endowments, the National Identification Service, in particular J. Poirier, E.C. Becker, A. Davies, A. Smetana, Y. Bousquet, L. LeSage and J. Denis for all the hours they spent identifying some of my specimens, my friends, family and colleagues who supported me and made this degree far more enjoyable, my supervisory committee, Dr. J. Borden, Dr. K. Lertzman and Staff Sergeant R. Stair (Retired) for their support and guidance, and especially Dr. Gail Anderson, for constant support, guidance and friendship. Without her, this degree would not have been possible.

TABLE OF CONTENTS

TITLE PAGE i

APPROVAL PAGE ii

ABSTRACT iii

DEDICATION iv

QUOTATION v

ACKNOWLEDGEMENTS vi

TABLE OF CONTENTS vii

LIST OF TABLES ix

LIST OF FIGURES x

1. INTRODUCTION 1

1.1 OBJECTIVES 2
1.2 RESEARCH AREAS 3
1.3 EXPERIMENTAL PROTOCOL 4
1 3 1 Experimental Carcasses 4
1 3 2 CWH zone 5
1 3 3 SBS zone 5
1 3 4 Temperature and Biomass Loss Measurements 5
1.4 SAMPLING METHODS 6
1 4 1 Data Recording 7
1 4 2 On-Site Collection 7
1 4 3 Field Morgue Collection 8
1.5 QUANTITATIVE ANALYSES 9

2. RESULTS 11

2.1 TEMPERATURE 11
2.2 DECOMPOSITION RATE 16
2 2 1 Fresh Stage 16
2 2 2 Bloat Stage 18
2 2 3 Active Decay 18

2.2.4 Advanced Decay Stage 20
2.2.5 Dry/Remains Stage 20
2.3 BIOMASS LOSS 21
2.4 INSECT DIVERSITY 21
2.5 INSECT SUCCESSION 28
2.5.1 Immediate burial *vs.* above-ground 28
2.5.2 Immediate *vs.* delayed burial 38
2.5.3 Immediate *vs.* disturbed burial 39

3. DISCUSSION 40

3.1 DIVERSITY IN EPHEMERAL HABITATS 40
3.2 SUCCESSION 43
3.2.1 Immediately buried carcasses 43
3.2.1.1 Dipteran carrion fauna 43
3.2.1.2 Coleopteran carrion fauna 46
3.2.1.3 Hymenopteran carrion fauna 46
3.2.2 Carcasses buried after 48 hours 47
3.2.3 Disturbed burial 48
3.3 Ecological Roles of Carrion Fauna 48
3.4 FORENSIC IMPLICATIONS 49
3.4.1 Elapsed Time Since Death 49
3.4.2 Temperature 50
3.4.3 Indicator species 51
3.4.3.1 Family Calliphoridae 51
3.4.3.2 Family Muscidae 53
3.4.3.3 Family Fanniidae 53
3.4.3.4 Family Phoridae 54
3.4.3.5 Family Sphaeroceridae 54
3.4.3.6 Family Heleomyzidae 54
3.4.3.7 Coleopteran Families 54
3.4.4 Recommendations 55

4. REFERENCES 57

LIST OF TABLES

Table 1. Linear regression analysis of temperature data collected during decomposition of pig carcasses in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia, June 1995 to October 1996 17

Table 2. Decompositional stages of pig carcasses buried immediately, buried 48 h after death, buried then disturbed and left above ground in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia 19

Table 3. Simpson's index of diversity, comparing the relative abundance of each insect species collected on pig carcasses after death, in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia. An index of one indicates a highly diverse community, while an index of zero indicates a community with no diversity 25

Table 4. Succession of insect species collected through exhumation (Ex) and pitfall traps (Pt) on buried and above-ground pig carcasses in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia. A = adults, P = pupae, PC = pupal cases, L = larvae, E = eggs, - = no collection possible 31

LIST OF FIGURES

Figure 1. Mean daily internal temperature of above-ground and buried pig carcasses measured every 90 min in the Coastal Western Hemlock (CWH) and in the Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia. Ambient air temperature in the CWH zone was recorded twice daily from the Malcolm-Knapp Research Forest weather station, 2 km from the research site. Ambient air temperature in the SBS zone was measured every 90 min at the research site....12

Figure 2. Mean daily internal buried pig carcass temperature in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia (estimated by grave temperature in the CWH zone) measured every 90 min from November 1995 (159 days since death) to October 1996. Ambient air temperature in the CWH zone was recorded twice daily from the Malcolm-Knapp Research Forest weather station, 2 km from the research site. Ambient air temperature in the SBS zone was measured every 90 min at the research site....13

Figure 3. Mean daily ambient air temperature, ambient grave temperature and internal buried pig carcass temperature measured every 90 min for the first 90 days after death in the Sub-boreal Spruce (SBS) biogeoclimatic zone of British Columbia. Day 0 = 10 June 1995....14

Figure 4. Maximum and minimum ambient air temperatures recorded twice daily from the Malcolm-Knapp Research Forest weather station and maximum and minimum internal buried pig carcass temperatures measured every 90 min for the first 90 days after death in the Coastal Western Hemlock (CWH) biogeoclimatic zone, British Columbia. Day 0 = 17 June 1995....15

Figure 5. Percent weight loss during decomposition, in above-ground and immediately buried pig carcasses in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia. Data from above-ground carcasses taken from Dillon and Anderson (1995)....22

Figure 6. Species abundance (dominance) compared with species richness (diversity) plots of insect communities on pig carcasses in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia....23

Figure 7. Relative abundance (ranked in order of increasing diversity from left to right) of the five most abundant species within four communities of insects collected from pig carcasses in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia....26

Figure 8. Species richness (within order and family) of insect communities collected from pig carcasses buried immediately and pig carcasses above ground in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia 27

Figure 9. Average linkage clustering of insect communities, based on the presence and absence of species collected from carcasses in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia 29

1. INTRODUCTION

Decomposing bodies constitute a rapidly changing habitat. After death, carrion undergo rapid physical, chemical and biological changes during the decomposition process. At each stage of decomposition, carrion is attractive to different species of insects. These insects colonize the remains in a predictable sequence, so that an analysis of the arthropods on a human homicide victim, weeks or months after death, can lead to an accurate estimate of elapsed time since death. This information may be vital in a homicide investigation (Anderson and VanLaerhoven 1996)

The succession of insect species on carrion varies according to temperature, habitat and geographic location (Reed 1958, Payne 1965, Denno and Cothran 1976, Goddard and Lago 1985, Greenberg 1985, Goff *et al* 1986, Goff and Odom 1987, Goff *et al* 1988, Goff 1991, Goff and Flynn 1991, Anderson and VanLaerhoven 1996). This variation occurs on both above-ground and buried carcasses (Rodriguez and Bass 1985, Smith 1986), but the location of the remains influences the time required for insects to locate a carcass, the sequence of colonization and the rate of decomposition (Payne *et al* 1968, Rodriguez and Bass 1985, Smith 1986). This variation makes extrapolation of insect succession databases between habitats and geographic locations extremely difficult. However, it is hypothesized that once insects locate buried remains, they will feed and develop normally, and will colonize in a predictable sequence

No experimental research into insect succession on buried corpses has been done in Canada. In fact, there has been no published experimental research on insect succession on buried corpses which accurately mimics a homicide scenario anywhere in the world.

1.1 OBJECTIVES

This research was designed to mimic three homicide scenarios accurately: immediate burial, delayed burial (many perpetrators do not dispose of the body immediately), and disturbed burial (perpetrators often return to and disturb the site of a forensic burial).

The specific objectives were:

1) to examine the successional biodiversity in insect species on immediately buried carrion in two biogeoclimatic zones, the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) zones of British Columbia (Meidinger and Pojar 1991),
2) to determine the effect of delayed burial on the successional biodiversity of insect species on buried carrion,
3) to determine the effect of disturbance on the successional biodiversity of insect species on buried carrion, and
4) to establish a database of insect succession on buried carrion in both the CWH and SBS zones (characteristic of the Vancouver and Cariboo Regions, respectively) of British Columbia for use in homicide investigations.

1.2 RESEARCH AREAS

Experimental areas were located in the CWH zone within the Vancouver Forest Region and the SBS zone within the Cariboo Forest Region. Most of the research was concentrated in the CWH zone since most buried corpses are found there (Anderson 1995). Only immediately buried and disturbed carcasses were studied in the SBS zone in conjunction with extensive exposed carcass experiments conducted at the same time (Dillon 1997). The research areas were located in the University of British Columbia's (U.B.C.) Alex Fraser Research Forest, Gavin Lake Block just east of Williams Lake in the Cariboo Forest Region and in U.B.C.'s Malcolm-Knapp Research Forest in Maple Ridge in the Vancouver Forest Region, where above-ground carcass experiments had been conducted in 1994 (Dillon and Anderson 1995). Both areas were chosen on the basis of representative soil type and vegetation.

Two weeks before carcass placement, 250 mL glass jar pitfall traps containing soapy water were placed at each planned carcass site and at three control sites (no carcass), at least 15 m from the carcass sites. After burial, the pitfall traps were placed in the soil above the carcasses to trap a sample of the insects attracted to or leaving the remains. The control pitfall traps remained at their original sites.

At each site graves were dug with a shovel on the same day, deep enough to allow the upper surface of a carcass to lie approximately 30 cm below the forest floor. All graves were at least 15 m away from the next grave or above-ground carcass, so that olfactory orientation of insects to each carcass was minimally influenced.

1.3 EXPERIMENTAL PROTOCOL

1.3.1 Experimental Carcasses

Twenty-three kg (50 lb) pigs (*Sus scrofa* L.) were used as surrogate human models, as these are considered to be excellent models for human decomposition (Catts and Goff 1992). A 15 cm pin gun shot to the head was used to kill all the pigs. To allow insertion of temperature probes, the carcasses were shot a second time, in the side of the thorax using a .22 caliber rimfire bullet. This produced a small entrance wound just wide enough to allow insertion of the probe, but did not produce an exit wound. Because clothing influences insect succession (Dillon and Anderson 1995) and most homicide victims are clothed or have cloth associated with the body (Anderson pers. com.), each carcass was identically clothed with underwear, a T-shirt, blouse, shorts and socks. For immediate and disturbed burial treatments, a freshly killed pig was placed in each grave within hours of death and the grave was filled to ground level with loosely packed soil. The top of each grave was disguised with branches, leaves and rocks. Pigs in delayed burial treatments were identically buried 48 h after death. Above-ground carcasses were protected from large scavenger attack by wire mesh (4"x2", 12.5 gauge) staked to the ground over the entire carcass. Buried carcasses were protected by wire mesh staked down over the grave.

1.3.2 CWH zone

On 17 June 1995, 15 pigs were buried immediately after death (within 5 h of death) Three of these pigs were exhumed at each of 2 and 6 weeks and 3, 11 and 16 months after death Nine pigs were buried 48 h after death Three of these pigs were exhumed at 2 and 6 weeks, and 3 months after death Three control pigs were left above ground and were examined at the same time as the exhumed pigs

1.3.3 SBS zone

On 10 June 1995, 12 pigs were buried immediately after death (within 8 h of death) Three of these pigs were exhumed at each of 2 and 6 weeks, and 3 and 16 months after death Three pigs exhumed at 2 weeks after death, were re-buried after sampling to determine the effect of disturbance They were again exhumed at 6 weeks after death and compared with the three pigs exhumed for the first time at 6 weeks after death Three control carcasses were left above ground and were examined at 2 weeks after death They were then consumed by a large scavenger and could not be sampled again

1.3.4 Temperature and Biomass Loss Measurements

Internal carcass temperature was taken from one above-ground carcass and one buried carcass (the last to be exhumed) within each biogeoclimatic zone Ambient air and soil temperature (from soil adjacent to the buried carcass) was recorded in both zones Temperatures were recorded using two types of dataloggers Double channel dataloggers (SmartReader 1®, Young Environmental Systems, Richmond, B.C.) measured the temperature every 30 min. Single channel dataloggers (Hobo®, Hoskins Scientific, Vancouver, B.C.) measured the temperature every 90 minutes. Failure of all but one Hobo® and several SmartReaders® precluded recording of additional internal carcass, ambient air or soil temperatures. Ambient air temperature data in the CWH zone were lost due to these failures, thus ambient air temperature data were taken from an Environment Canada weather station in the Malcolm-Knapp Research Forest, 2 km south of the research site.

Biomass loss was measured by placing an exhumed carcass on a mesh platform and weighing it using a 70 kg (150 lb) scale on a pulley system. Above-ground carcasses were not weighed, because the disturbance could have affected the succession pattern since the carcasses were not on mesh platforms

1.4 SAMPLING METHODS

At each sampling date, insects in each pitfall trap were separated from the soapy water by the use of a small tea strainer and placed in 70% ethanol in a sterile 100 mL vial. Fresh soapy water was then placed in each pitfall trap. Insect species that were collected in equal abundance from control and carcass sites were excluded because these were considered to be endemic species that are not associated with carrion

The buried carcasses were exhumed carefully, in the manner of crime scene investigations and examined for insects. The exhumation consisted of three components: data recording, on-site collection and field morgue collection. When insects were sampled, 10-20 individuals per species were routinely collected. All individuals of less numerous species were also collected.

1.4.1 Data Recording

Extensive photographic records during all stages of exhumation were supplemented by written notes of all observations. These were made with reference to a 1x1 m grid, with four 50 cm^2 quadrats, laid out before the excavation.

1.4.2 On-Site Collection

Collection of insects began with careful removal of surface plants. They and the exposed ground were examined visually for insects. Next, soil was removed systematically, one quadrat at a time moving from the outermost to the innermost area (Skinner and Lazenby 1983). Soil was sorted by hand and visually inspected for insects, samples of which were collected. When the entire corpse was exposed, photographs were taken and notes made, then the carcass was lifted out of the grave and moved away on a mesh platform. Soil in the bottom of the grave was examined visually and samples of all insect species were collected.

1.4.3 Field Morgue Collection

The entire exhumed carcass, as well as all areas of the clothing, including pockets, were examined and sampled for insects using forceps or gloved fingers The carcass was then placed in a plastic bag and later disposed of by incineration Half of the larval Diptera were preserved in 70% ethanol in screw cap vials, while the rest were kept alive in sterile 250 mL vials containing some beef liver or pork with a paper towel lid affixed by an elastic band These were reared to adulthood in the laboratory, facilitating identification Adult insects were pinned and larval insects were labeled and preserved in 70% ethanol for later identification

All larval Calliphoridae and Muscidae were examined under a binocular microscope to determine instar by number of spiracular slits (Smith 1986) Insects were identified using keys and comparisons with verified specimens in the Simon Fraser University forensic insect reference collection Specimens that were difficult to identify were sent to the National Identification Service in Ottawa for identification and to provide voucher specimens for our reference collection

Above-ground control carcasses were sampled in a similar manner on each exhumation day, but on a lesser scale because above-ground succession can be determined from the established database (Dillon 1997)

1.5 QUANTITATIVE ANALYSES

Only insects collected from the grave soil or on the carcasses were used in the quantitative analyses Therefore insects collected in pitfall traps were only used in the succession table Simpson's index of diversity (1-D) (Krebs 1989), defined as 1- (the probability of picking two organisms that are the same species) or

$$1 - D = 1 - \sum (p_i)^2$$

where p_i = the proportion of individuals of species i in the community, was calculated using the relative abundance of each species within the different treatments This index gives a measure of diversity of insect species, in which a score approaching 1 indicates high diversity

I compared the similarity or difference in species composition between treatments using average linkage clustering (Minitab 1994) Treatments that are most similar in species composition have the highest scores and are clumped closest together in the cladogram A score of 100 means that the two treatments being compared had identical species compositions Using average linkage clustering, the distance between two clusters (or treatments) is the mean distance between a variable (species a) in one cluster and the same variable in the other cluster (Minitab 1994) Therefore, two treatments composed of identical species will have no distance between them on the cladogram and will have a similarity of 100 The distance matrix (d_{mj}) is calculated by

$$d_{mj} = (N_k d_{kj} + N_l d_{lj}) / N_m$$

where N_k, N_l, N_m = the number of variables in the clusters k, l and m

The correlation distance is calculated by

$$d_{ij} = 1 - \rho_{ij}$$

where ρ_{ij} = the Pearson product moment correlation between variables i and j

I used Microsoft Excel (Microsoft 1985) to calculate the linear regression equations predicting internal carcass temperature from ambient air temperature and soil temperature and predicting soil temperature from ambient air temperature The temperature data for the first three days after death were omitted to eliminate the effect of *algor mortis*

2. RESULTS

2.1 TEMPERATURE

Differences were observed between the ambient air and grave soil temperatures and between the internal carcass temperatures of buried and above-ground pigs. These trends held true for carcasses in both study sites. In both zones, buried carcasses did not show the same internal temperature spike experienced by above-ground, carcasses (Figure 1). During the winter months in the SBS zone, internal buried carcass temperature did not fluctuate with ambient air temperature (Figure 2). However, during the winter months in the CWH zone, the internal buried carcass temperature (estimated by grave temperature[1] because the datalogger failed) did fluctuate significantly ($r^2 = 0.73$, $P < 0.0001$) with the ambient air temperature recorded at the Malcolm-Knapp Research Forest weather station (Figure 2).

There was less fluctuation in soil than in ambient air temperature overall, as illustrated by data collected in the SBS zone (Figure 3). After *algor mortis* was complete, there was little difference between grave temperature and internal carcass temperature. In both zones, diurnal fluctuations were much greater in the ambient air temperature, than in the internal buried carcass temperature, as illustrated by data collected in the CWH zone (Figure 4).

---

[1] The use of grave temperature is justified by the strong relationship between internal carcass and grave temperatures recorded for 262 days from the SBS zone ($r^2=0.92$, $P <0.0001$).

Figure 1. Mean daily internal temperature of above-ground and buried pig carcasses measured every 90 min in the Coastal Western Hemlock (CWH) and in the Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia. Ambient air temperature in the CWH zone was recorded twice daily from the Malcolm-Knapp Research Forest weather station, 2 km from the research site. Ambient air temperature in the SBS zone was measured every 90 min at the research site.

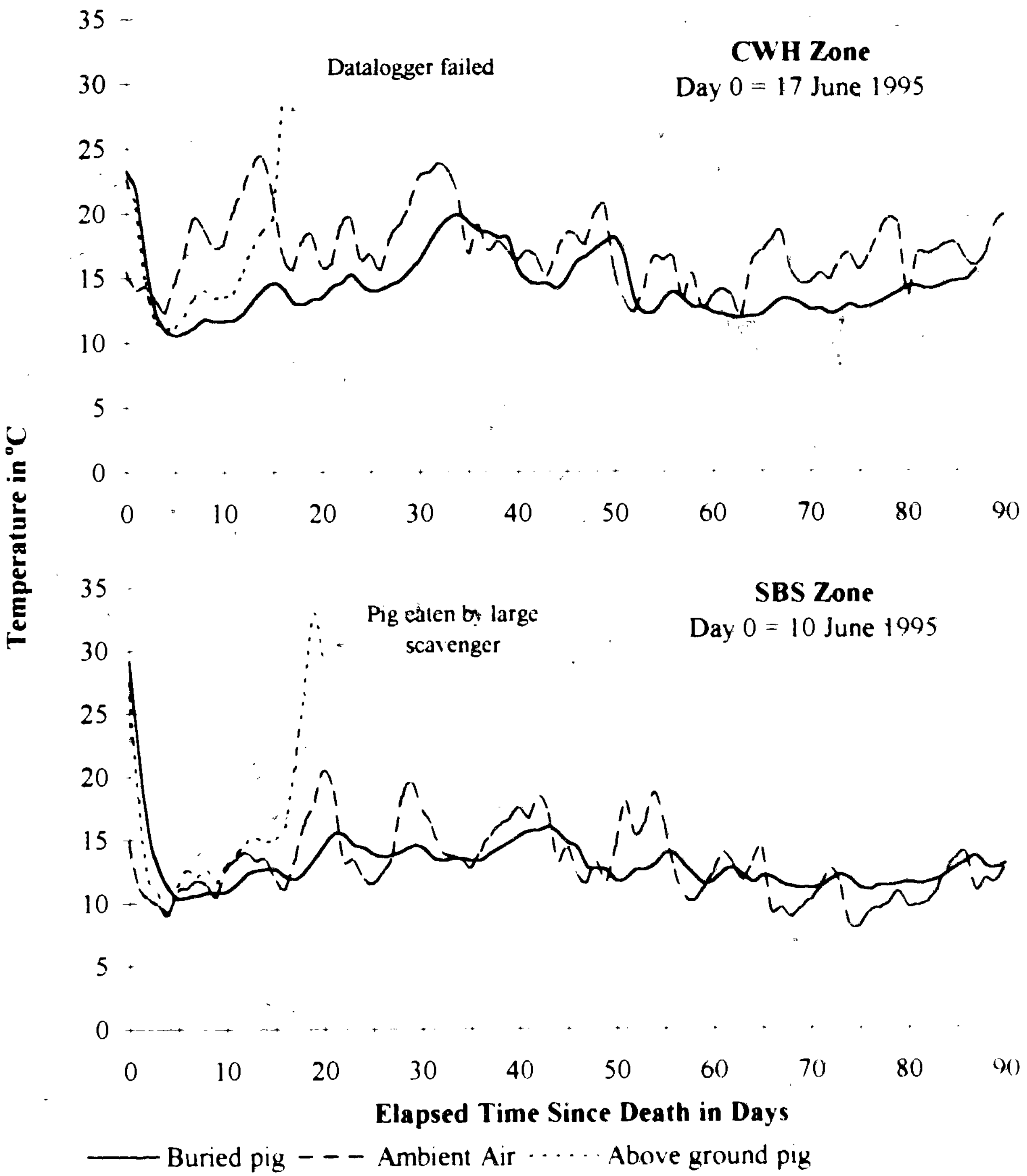


Figure 2. Mean daily internal buried pig carcass temperature in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia (estimated by grave temperature in the CWH zone) measured every 90 min from November 1995 (159 days since death) to October 1996. Ambient air temperature in the CWH zone was recorded twice daily from the Malcolm-Knapp Research Forest weather station, 2 km away from the research site. Ambient air temperature in the SBS zone was measured every 90 min at the research site.

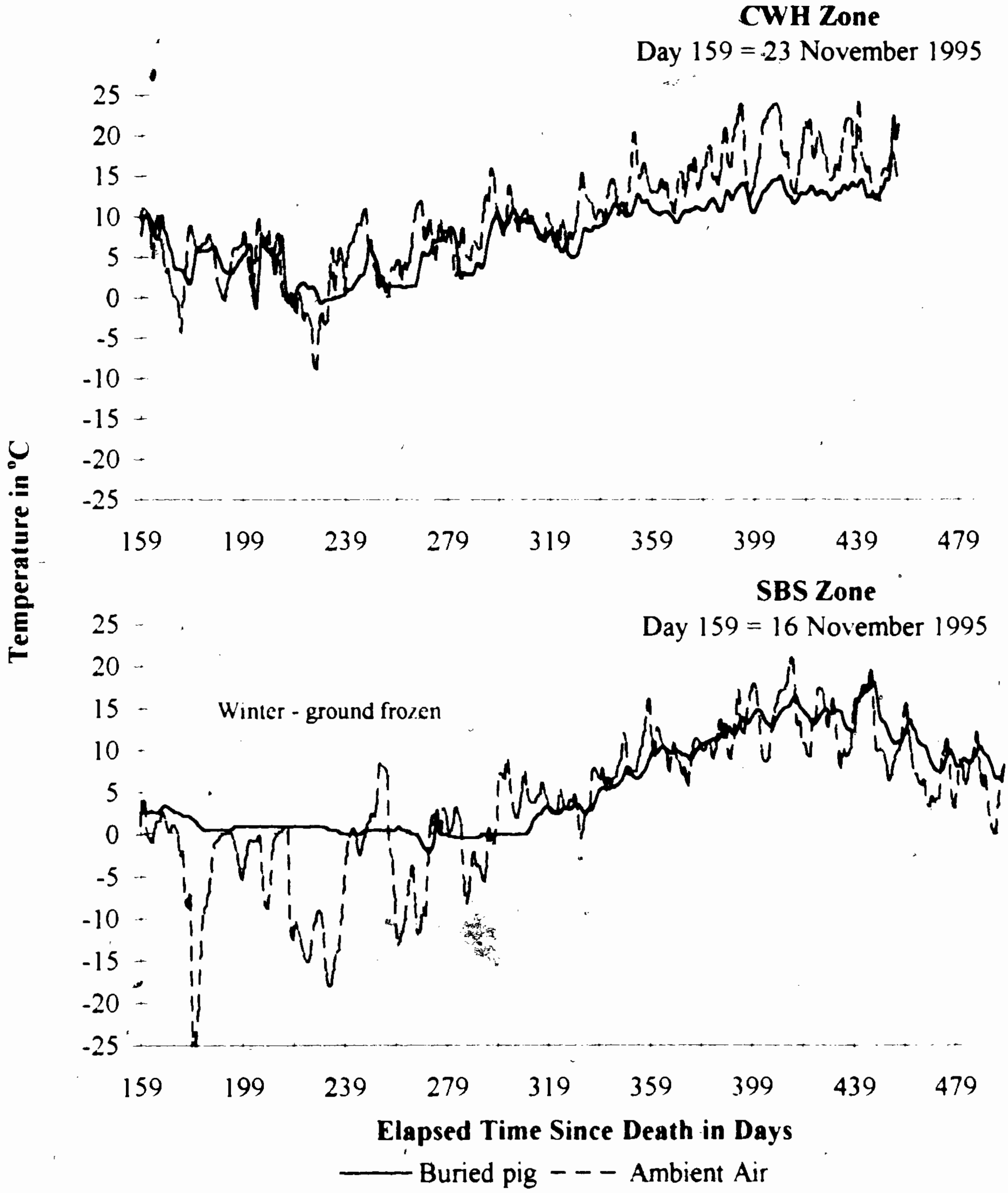


Figure 3. Mean daily ambient air temperature, ambient grave temperature and internal buried pig carcass temperature measured every 90 min for the first 90 days after death in the Sub-boreal Spruce (SBS) biogeoclimatic zone of British Columbia. Day 0 = 10 June 1995.

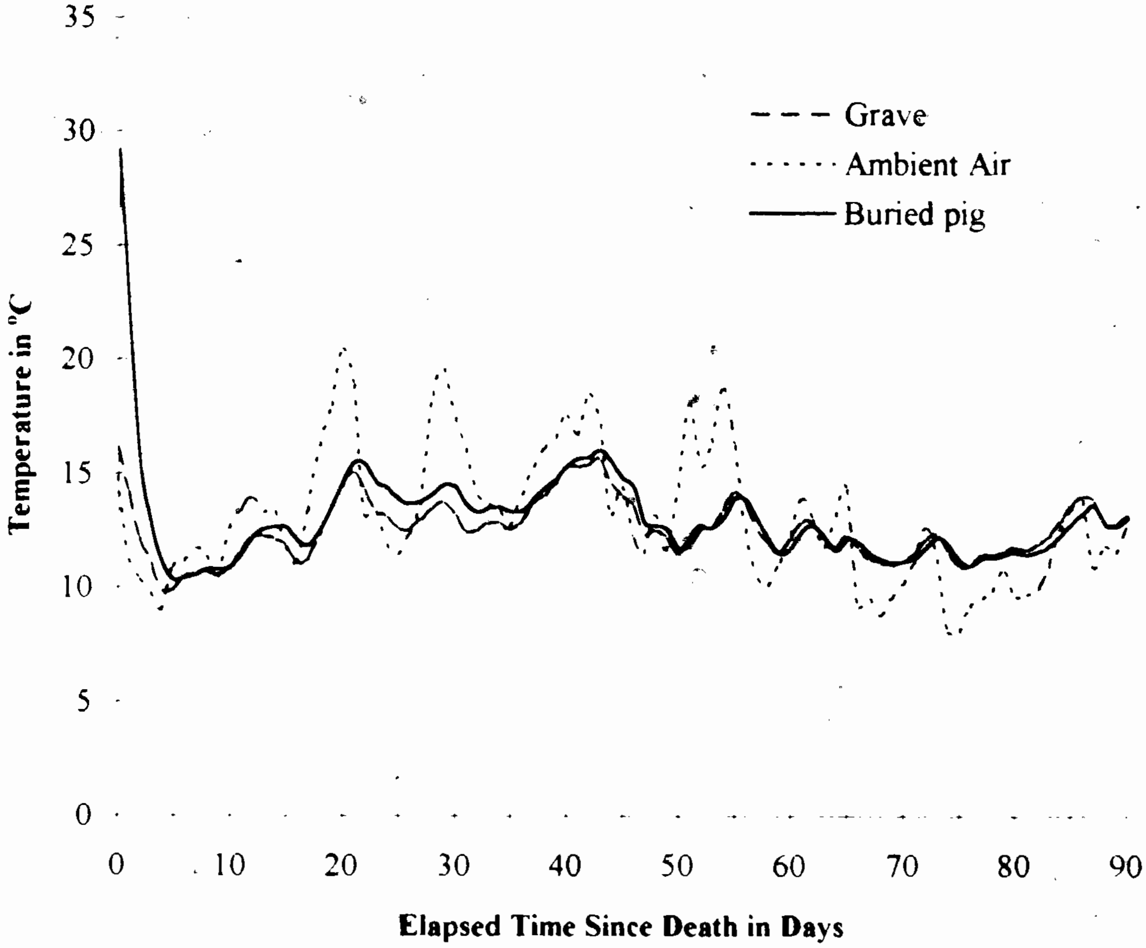
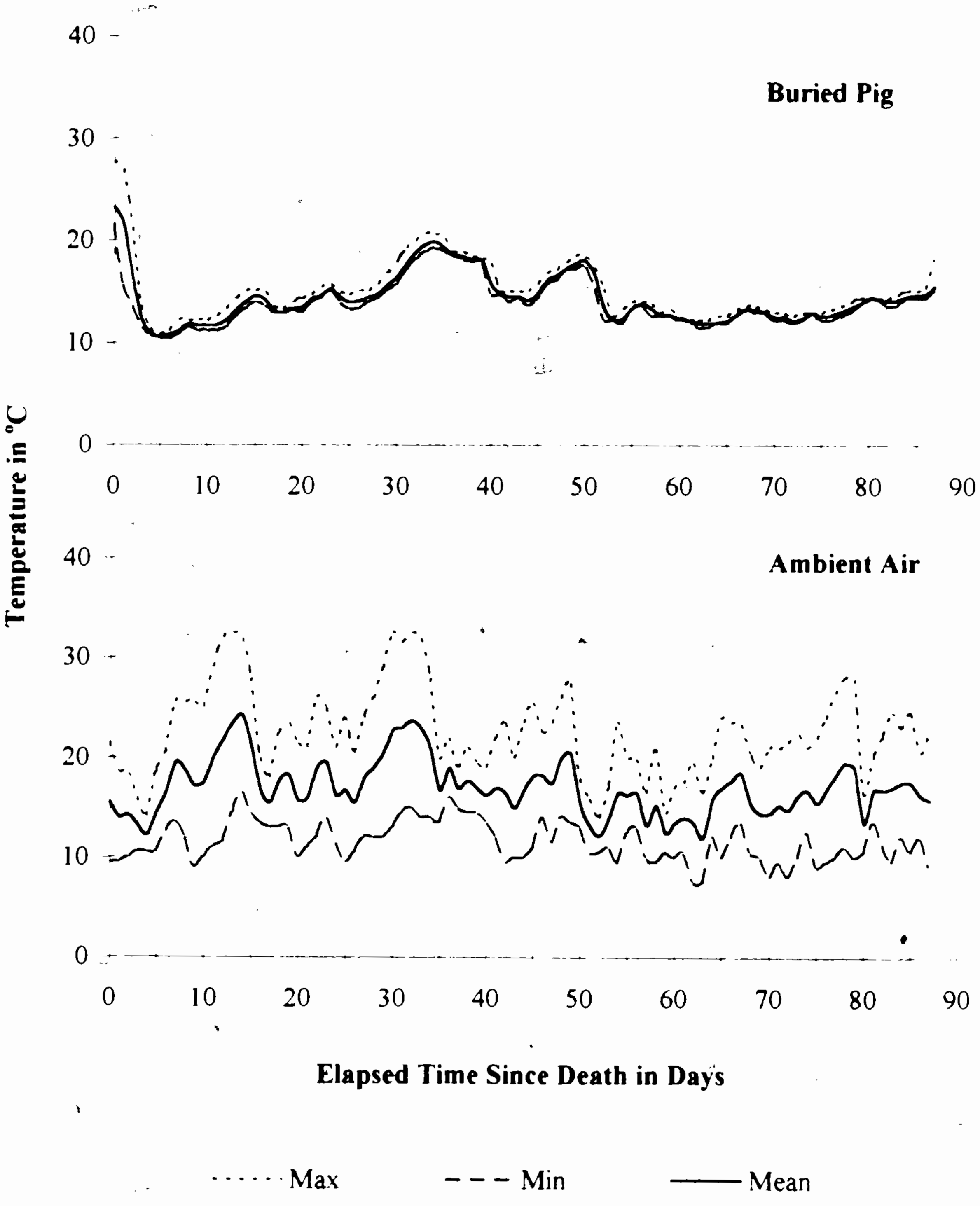


Figure 4. Maximum and minimum ambient air temperatures recorded twice daily from the Malcolm-Knapp Research Forest weather station and maximum and minimum internal buried pig carcass temperatures measured every 90 min for the first 90 days after death in the Coastal Western Hemlock (CWH) biogeoclimatic zone, British Columbia. Day 0 = 17 June 1995.



Weather station ambient air temperature was not a good predictor of the internal temperature of above-ground carcasses in the CWH zone, although it was a good predictor of the internal temperature of above-ground carcasses in the SBS zone before the action of the maggot masses increased the internal temperature (Table 1) Soil temperature was an excellent predictor of internal buried carcass temperature in the SBS zone (Table 1) Mean and minimum ambient air temperatures were also acceptable predictors ($r^2 > 0.5$) of internal buried carcass temperature in the SBS zone, but only in the spring, summer and fall months (Table 1) In contrast, ambient air temperature taken from a weather station 2 km away was not a good predictor ($r^2 < 0.5$) of internal buried carcass temperature in the CWH zone, likely due to small sample size, although it was an acceptable predictor of grave temperature (Table 1)

2.2 DECOMPOSITION RATE

The rate of decomposition of buried carcasses was considerably slower than for the above-ground carcasses Although decomposition is continuous, Payne *et al.* (1968) recognized five stages of physical decomposition, which I have adapted to characterize the experimental carcasses

2.2.1 Fresh Stage

This stage began at death and continued until bloating of the carcasses was visible This stage was not observed after the initial placement of the carcasses since

Table 1. Linear regression analysis of temperature data collected during decomposition of pig carcasses in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia, June 1995 to October 1996

Dependent temperature variable	Biogeoclimatic zone and days since death	Independent temperature variable	N	Slope	y intercept	r^2	*P*
Internal, buried carcass	SBS, days 3-94, 327-490 (spring, summer, fall)	Maximum daily soil	262	1.13	-1.33	0.9	< 0.0001
		Minimum daily soil	262	1.13	-0.4	0.92	< 0.0001
		Mean daily soil	262	1.14	-0.86	0.92	< 0.0001
		Maximum daily air	262	0.34	5.94	0.36	< 0.0001
		Minimum daily air	262	0.62	7.2	0.53	< 0.0001
		Mean daily air	262	0.59	4.9	0.6	< 0.0001
	SBS, days 159-326 (winter)	Maximum daily soil	167	0.68	0.45	0.64	< 0.0001
		Minimum daily soil	167	0.83	0.38	0.8	< 0.0001
		Mean daily soil	167	0.78	0.39	0.77	< 0.0001
		Maximum daily air	167	0.023	0.97	0.02	0.08
		Minimum daily air	167	0.024	0.9	0.02	0.04
		Mean daily air	167	0.024	0.93	0.02	0.05
	CWH, days 3-88 (summer, fall)	Maximum weather station	85	0.16	11.23	0.09	0.0055
		Minimum weather station	85	0.66	6.12	0.37	< 0.0001
		Mean weather station	85	0.35	8.25	0.19	< 0.0001
Soil	CWH, days 120-461 (fall, winter, spring, summer)	Maximum weather station	341	0.47	2.01	0.64	< 0.0001
		Minimum weather station	341	0.63	3.94	0.71	< 0.0001
		Mean weather station	341	0.58	2.29	0.73	< 0.0001
Internal, above-ground carcass	SBS, days 3-22 (summer)	Maximum daily air	19	0.42	9.84	0.79	< 0.0001
		Minimum daily air	19	0.29	4.83	0.37	0.001
		Mean daily air	19	0.4	6.4	0.83	< 0.0001
	CWH, days 3-18 (summer)	Maximum weather station	15	0.26	11.46	0.059	0.38
		Minimum weather station	15	0.94	1.8	0.37	0.016
		Mean weather station	15	0.47	6.74	0.14	0.16

both above-ground carcasses and buried carcasses had passed beyond this stage by two weeks after death (Table 2)

2.2.2 Bloat Stage

By 2 weeks after death above-ground carcasses had passed the bloat stage (Table 2), characterized by the accumulation of gases within the body as anaerobic bacteria within the gut begin to digest the carcass This was evidenced by the deflated nature of the carcasses However, buried bodies decompose at a much slower rate, allowing characterization on the basis of disarticulation By 2 weeks after death, buried carcasses had entered a primary bloat stage (Table 2), characterized by both the bloated appearance and the lack of disarticulation By 6 weeks after death, buried carcasses were in a secondary bloat stage (Table 2), still bloated, but with the limbs disarticulated

2.2.3 Active Decay

This stage was characterized by the deflation of the carcass and disarticulation of the head Flesh and skin were still present By 2 weeks after death, the above-ground carcasses were in this stage (Table 2), with large maggot masses rapidly consuming flesh The buried carcasses were in this stage by 3 months after death (Table 2) No maggot masses were present The abdomen was collapsing with the head and legs disarticulated The carcasses were very wet with a strong odour once they were removed from the grave

Table 2. Decompositional stages of pig carcasses buried immediately, buried 48 h after death, buried then disturbed, and left above ground in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia.

		Time taken to reach each stage of decomposition (days)					
Zone	Treatment	Fresh	Primary bloat	Secondary bloat	Active decay	Advanced decay	Dry / remains
CWH	Immediate burial	0	< 14	< 45	< 90	< 335	+ 490
	Delayed burial	0	< 14	< 45	< 90	n/a	n/a
	Above-ground	0	stage not observed		< 14	< 45	< 90
SBS	Immediate burial	0	< 14	< 45	< 90	< 490	+ 490
	Disturbed burial	0	n/a	< 45	n/a	n/a	n/a
	Above-ground	0	stage not observed		< 14	n/a	n/a

2.2.4 Advanced Decay Stage

At this point, most of the flesh had been removed, but skin, bone, fat and cartilage remained on above-ground carcasses, which had reached this stage by 6 weeks after death in the CWH zone (Table 2) The above-ground carcasses in the SBS zone had been eaten by a large scavenger by this time By 11 months after death, the buried carcasses in the CWH zone had reached the equivalent of this stage (Table 2) Some flesh remained, although some of it had turned to adipocere tissue, formed by the conversion of soft tissue to hydrolyzed fat in the presence of cool moist soil or water (Spitz and Fisher 1973) and the abdomen had collapsed The carcasses were still fairly wet At 16 months after death, the buried carcasses in the CWH zone were still in this stage (Table 2), with the remaining flesh turned to adipocere tissue and the ribcage collapsed, giving the carcasses a flattened appearance Buried carcasses in the SBS zone had reached the advanced decay stage by the time the experiment was terminated at 16 months after death (Table 2) They resembled the buried carcasses exhumed in the CWH zone at 11 months after death

2.2.5 Dry/Remains Stage

By 11 months after death, the above-ground carcasses had entered this final stage with only bone, cartilage and some skin remaining (Table 2) Bits of clothing and bones were the only remaining evidence of these carcasses

2.3 BIOMASS LOSS

Biomass loss in buried carcasses was slightly faster in the CWH zone than in the SBS zone (Figure 5). However, buried carcasses in both zones lost biomass much more slowly than above-ground carcasses in the shade in the spring of 1994 in the CWH zone (Dillon and Anderson 1995). The slower rate of decomposition and decreased rate of biomass loss lengthens insect succession on buried carcasses.

2.4 INSECT DIVERSITY

Diversity of insect species consists of both the species richness and the relative abundance of each species. Examining the dominance-diversity plots (Krebs 1989) (Figure 6) for above-ground carcasses in both the CWH and SBS zones, it is immediately apparent that these communities have low species richness compared with that on buried carcasses, and are dominated by a few species of high relative abundance. Although it appears that the above-ground community in the SBS zone is much less diverse than in the CWH zone, this was due to the small sample size since the carcasses were removed by a scavenger. Therefore, all the later species of insects that would have colonized these carcasses could not be included in the diversity calculation. Buried carcasses appear to have a more diverse community than above-ground carcasses, with greater species richness and evenness. Although it appears that disturbed burial carcasses have less species richness, this is due to the much smaller sample size compared with the other buried carcasses. There is no apparent difference

Figure 5. Percent weight loss during decomposition, in above-ground and immediately buried pig carcasses in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia. Data from above-ground carcasses taken from Dillon and Anderson (1995)

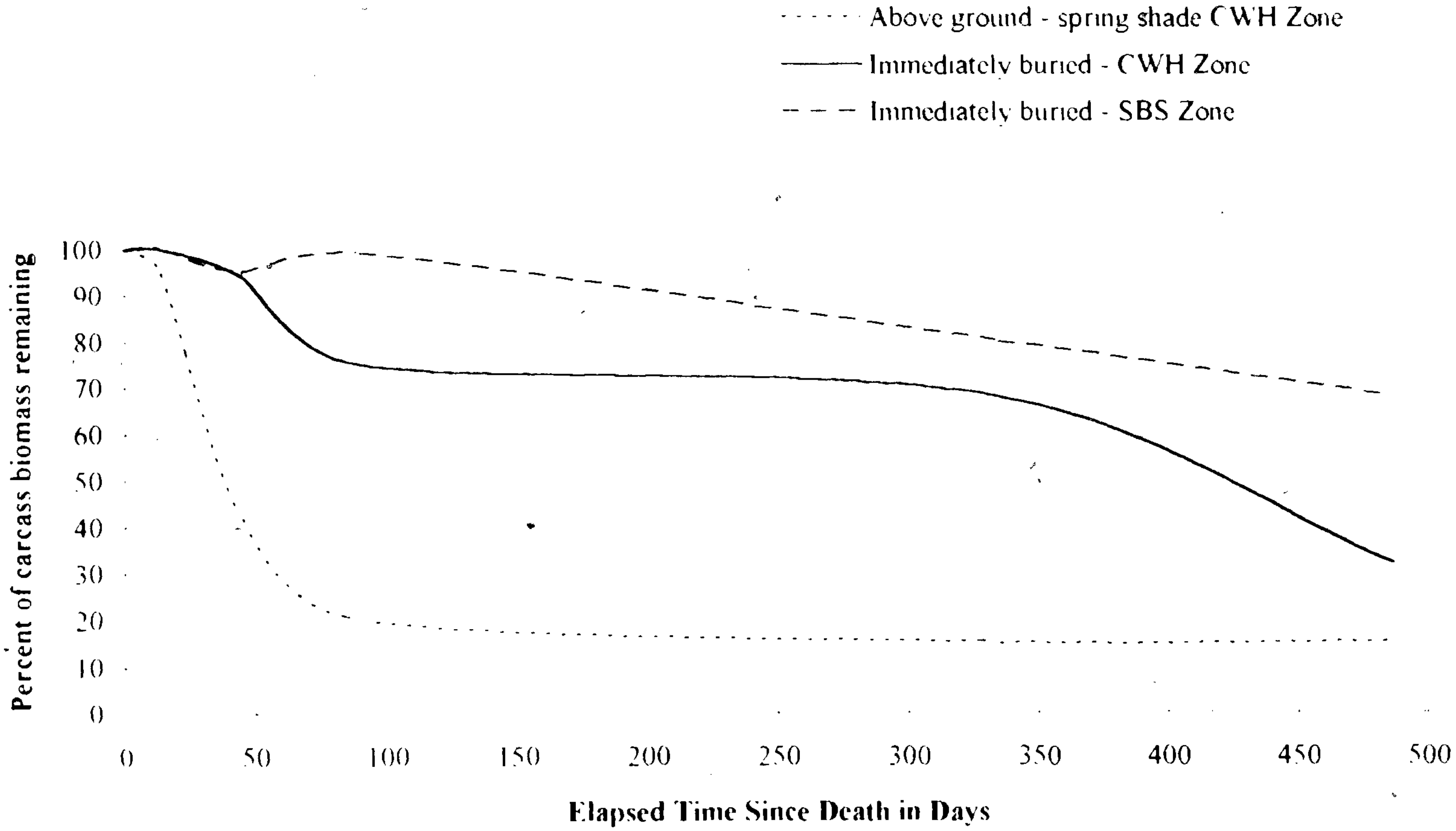
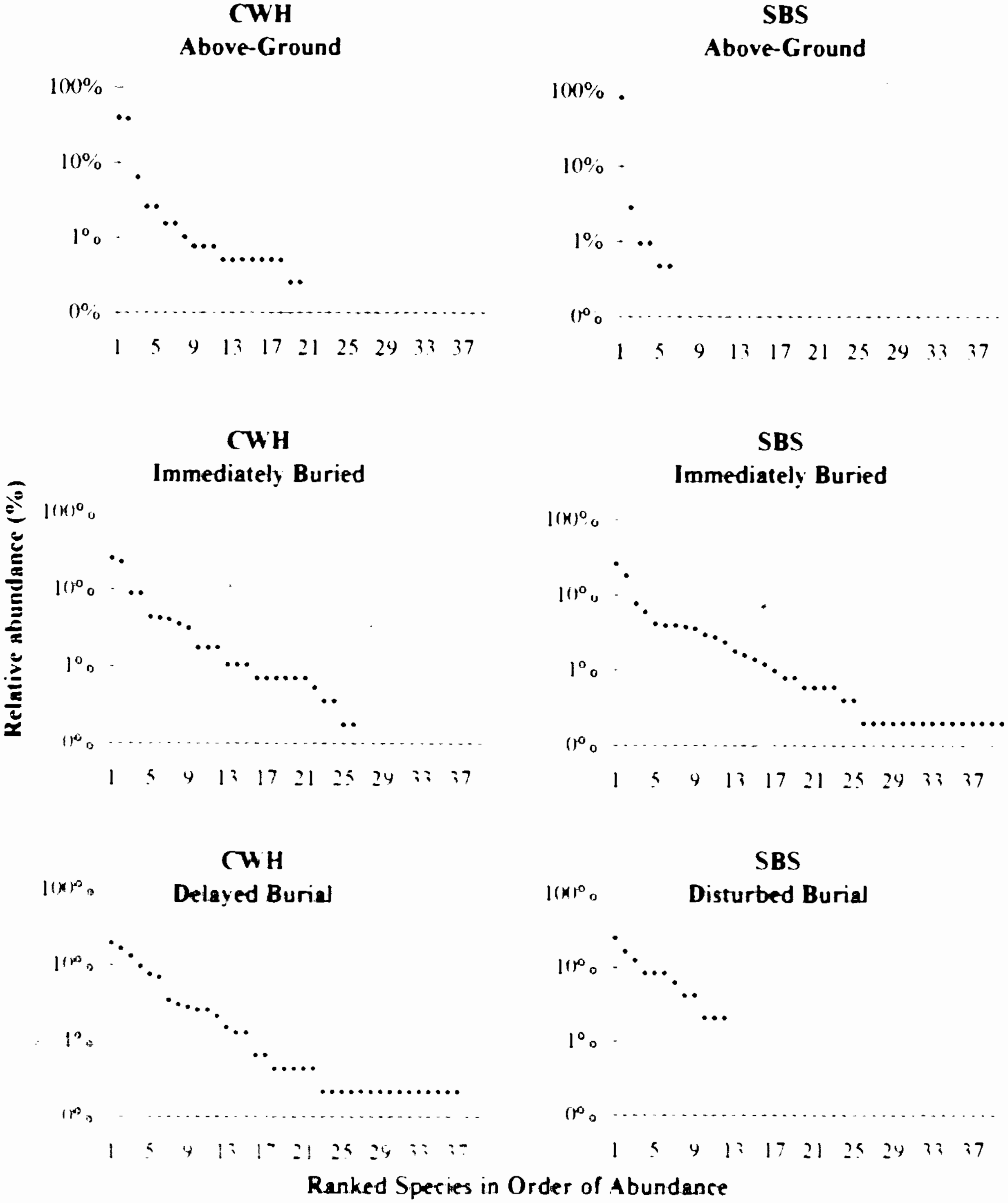


Figure 6. Species abundance (dominance) compared with species richness (diversity) plots of insect communities on pig carcasses in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia



in relative abundance of species between the different burial treatments This is confirmed by Simpson's index of diversity (Table 3)

Examining the relative abundance of the five most abundant species in burial and above-ground communities collected from carcasses (Figure 7), it is apparent that the community on the above-ground carcasses in the SBS zone is dominated by one species, *Phormia regina* (Meigen). The other three communities exhibit more evenness, although the community on the above-ground carcasses in the CWH zone is co-dominated by *Phormia regina* and *Lucilia illustris* (Meigen)

All four communities are composed of insects from two orders Diptera and Coleoptera (Figure 8) The species richness within different families from these orders is higher in the two communities on buried carcasses, than in the two above-ground carrion communities (Figure 8) Species richness is high in the family Staphylinidae (Coleoptera) for all four communities However, in the two buried carrion and in the above-ground CWH communities, other coleopteran families also have relatively high species richness The same trend is true with the dipteran families The dipteran family Calliphoridae plays a dominant role in the species richness of three communities, but not in the immediately buried CWH community Unlike the two above-ground communities, in the buried carrion communities, the family Muscidae is dominant There appears to be very little difference in the species richness of different families between the CWH and SBS zones Although the SBS above-ground

Table 3. Simpson's index of diversity, comparing the relative abundance of each insect species collected on pig carcasses after death, in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia. An index approaching 1 indicates a highly diverse community, while an index of zero indicates a community with no diversity.

Zone	Treatment	Simpson's index (1-D)
SBS	Above-ground	0.1
	Buried	0.9
	Disturbed	0.9
CWH	Above-ground	0.7
	Buried	0.9
	Delayed	0.9

Figure 7. Relative abundance (ranked in order of increasing diversity from left to right) of the five most abundant species within four communities of insects collected from pig carcasses in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia

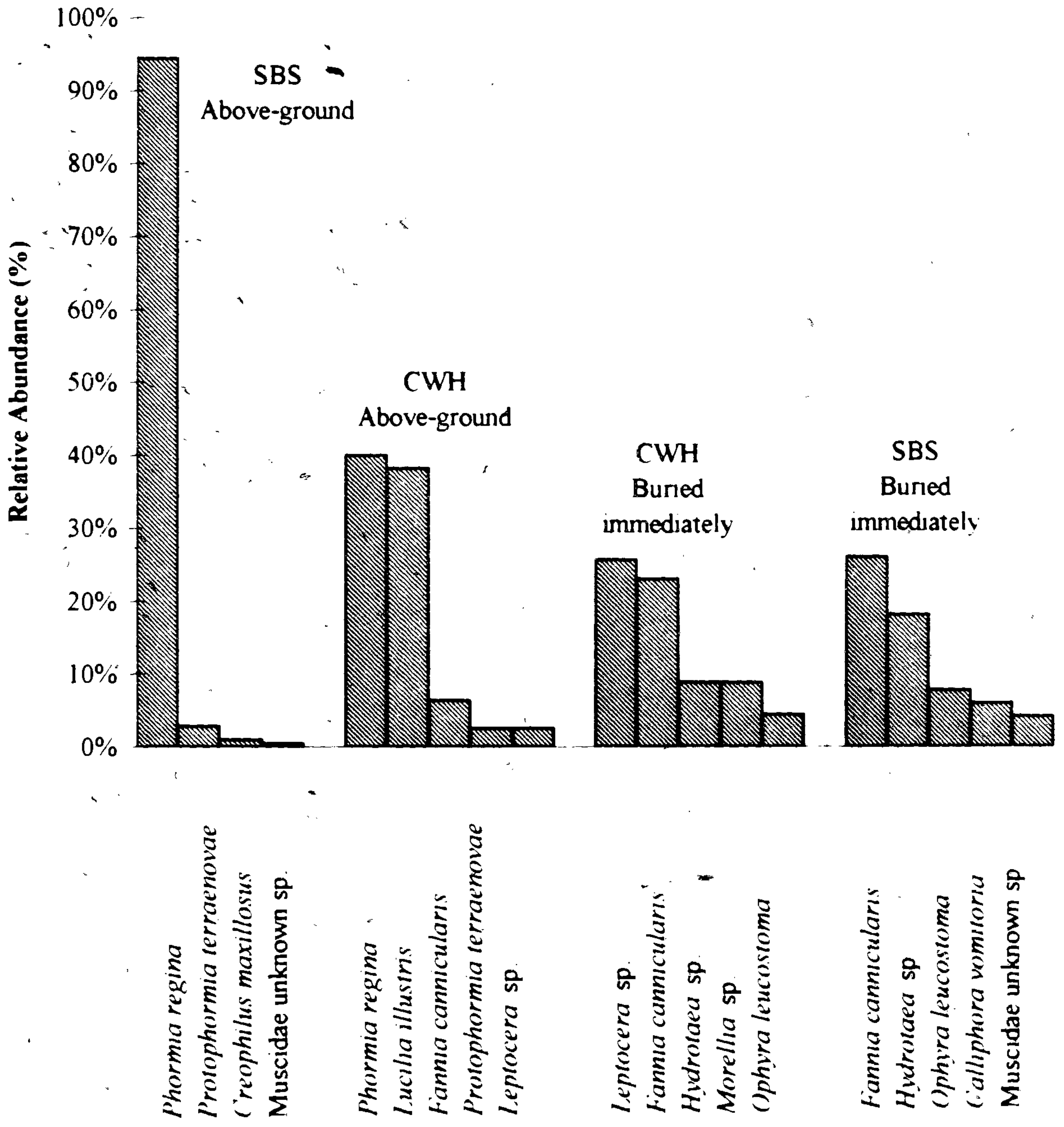
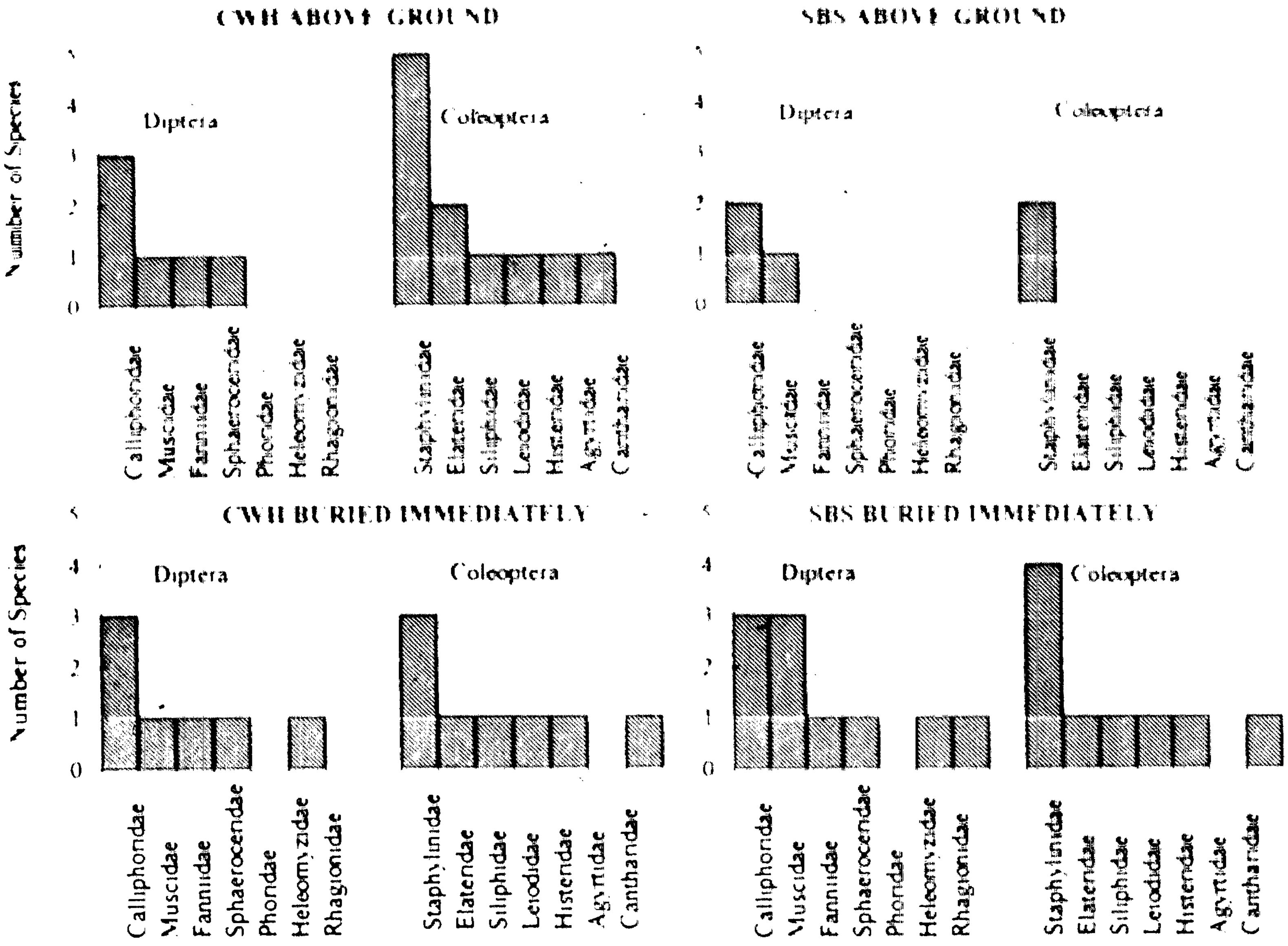


Figure 8. Species richness (within order and family) of insect communities collected from pig carcasses buried immediately and pig carcasses above ground in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia



community appears to have less species richness than the other three communities, this is due to small sample size.

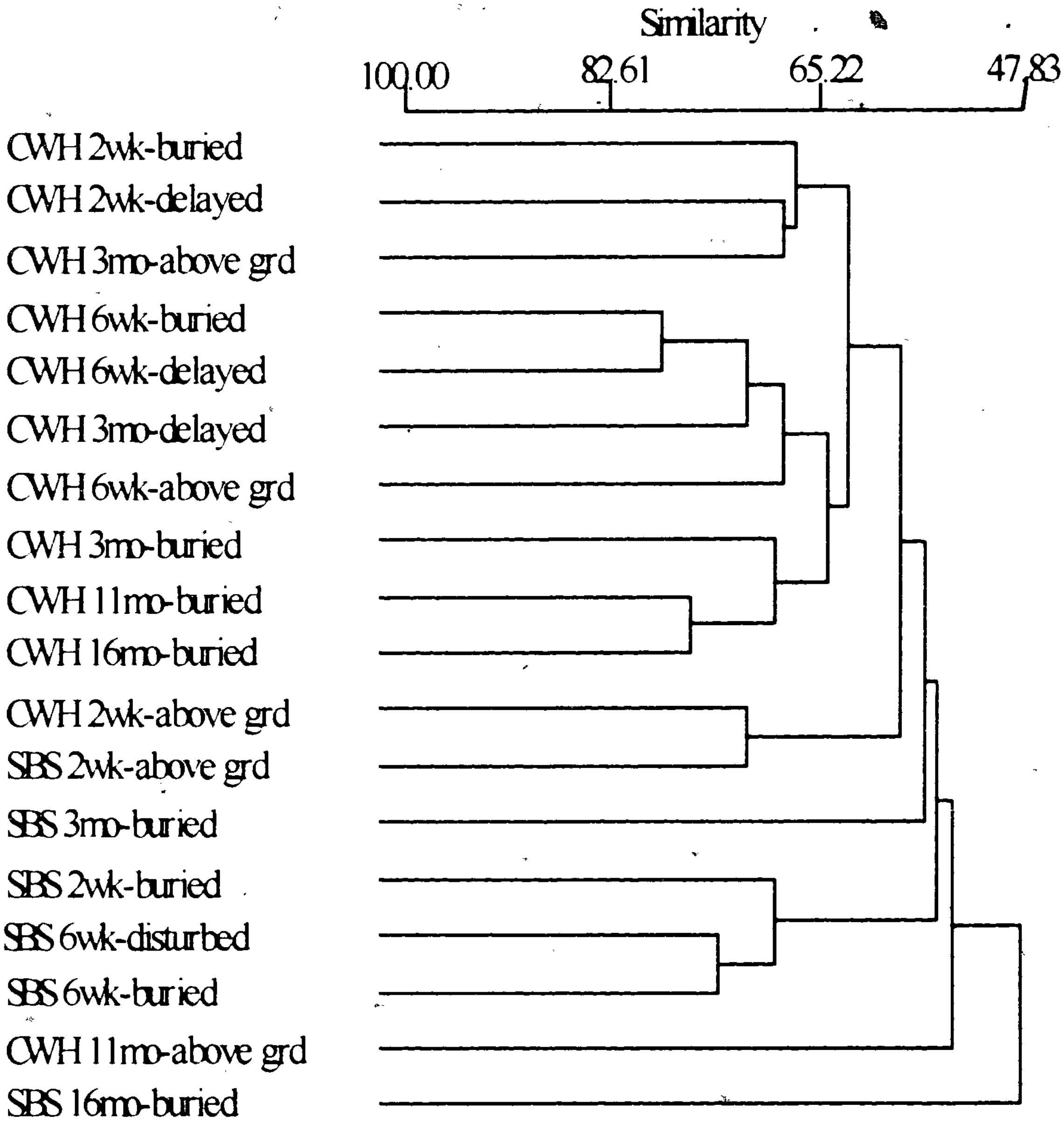
However, there is a difference in the species composition of the communities in the CWH and SBS zones when the different communities are compared using average linkage clustering (Figure 9), based on the presence and absence of the different species collected during different sampling dates. The communities in the SBS zone are more similar to each other in species composition, than they are to the communities in the CWH zone and *vice versa.* Both treatment and time since death appear to influence the degree of similarity in species composition between different communities. Within the CWH zone, the communities of insects collected from immediately and delayed buried carrion at 6 weeks after death are more similar to each other than they are to the community collected from above-ground carrion at 6 weeks after death (Figure 9). It is interesting to note that CWH and SBS communities of insects collected on above-ground carrion at 2 weeks after death were more similar to each other than to any other community, likely due to the dominance of blowfly species on these carcasses.

2.5 INSECT SUCCESSION

2.5.1 Immediate burial *vs.* above-ground

The following successional data are based on insects collected both through exhumation and pitfall trapping. At two weeks after death, the buried carcasses in both

Figure 9. Average linkage clustering of insect communities, based on the presence and absence of species collected from carcasses in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia.



zones were in the primary bloat stage (Table 2) I collected adults of several species of blowfly (Calliphoridae) from pitfall traps in both zones, but only *Calliphora vomitoria* (L) and *Lucilia illustris* larvae in the SBS zone on buried carcasses (Table 4) Adults of the families Muscidae, Sphaeroceridae, Phoridae and Sarcophagidae were collected from pitfall traps above buried carcasses in both zones Adults and pupae of *Fannia canicularis* (L) (Fanniidae) were collected in the SBS zone on buried carcasses and in pitfall traps, but only adults were collected in the CWH zone at this time I collected adult Staphylinidae, Silphidae and Leiodidae on buried carcasses and in pitfall traps in both zones Larval Staphylinidae and Histeridae were collected in the SBS zone on buried carcasses *Nasonia vitripennis* (Walker) (Pteromalidae) and *Camponotus herculeanus* (L) (Formicidae) adults were collected on buried carcasses and in pitfall traps in both zones

The immediately buried carcasses were in the secondary bloat stage by six weeks after death (Table 2) I collected pupae of *Eucalliphora latifrons* (Hough) (Calliphoridae) and *Ophyra leucostoma* (Wied) (Muscidae) from the immediately buried carcasses in the SBS zone (Table 4) Pupae of *Hydrotaea* sp and *Morellia* sp (Muscidae) as well as larvae, pupae and adults of *F. canicularis* were collected from buried carcasses in both zones *Dohrniphora* sp (Phoridae) larvae were collected from buried carcasses in the CWH zone I collected adults of these species in pitfall traps above the buried carcasses at the same time [illegible] species collected through exhumation (Ex) and pitfall traps (Pt) on buried and above-ground pig carcasses in the Coastal Western Hemlock (CWH) and Sub-boreal Spruce (SBS) biogeoclimatic zones of British Columbia. A = adults, P = pupae, Pt = pupal cases, L = larvae, E = eggs, - = no collection possible

Decomposition Stage	Order and Family	Genus and species	CWH Zone						SBS Zone					
			buried				above		buried				above	
			immediate		delayed		ground		immediate		disturbed		ground	
			Ex	Pt	Ex	Pt	Ex	Pt	Ex	Pt	Ex	Pt	Ex	Pt
		Time Since Death	2 wks		2 wks		n/a		2 wks		n/a		n/a	
[illegible]	DIPTERA													
	Calliphoridae	*Lucilia illustris* (Meigen)			prepupal		-	-	L		-	-	-	-
		Phormia regina (Meigen)		A			-	-			-	-	-	-
		Protophormia terraenovae (Robineau-Desvoidy)					-	-		A	-	-	-	-
		Calliphora vomitoria (L.)		- A			-	-	L		-	-	-	-
		Calliphora vicina Robineau-Desvoidy		A			-	-		A	-	-	-	-
		Calliphora terraenovae Macquart					-	-		A	-	-	-	-
		unknown sp.					-	-	L		-	-	-	-
	Muscidae	*Hydrotaea* sp		A			-	-		A	-	-	-	-
		Ophyra leucostoma (Wied.)				A	-	-		A	-	-	-	-
		unknown sp					-	-	L		-	-	-	
		unknown sp			L		-	-	L		-		-	
	Sphaeroceridae	*Leptocera* sp		A		A	-	-		A	-			
	Fanniidae	*Fannia canicularis* (L.)		A		A	-	-	P	A	-			
	Phoridae	*Dohrniphora* sp		A		A	-	-		A	-			
	Sarcophagidae	*Boettcheria* sp		A			-	-						
		Neobelleria cooleyi (Parker)					-	-		A				
	Rhagionidae	unknown sp	L				-	-	L					
	Family unknown	unknown sp			A			-						
		unknown sp					-	-	A					
		unknown sp					-		A					
		unknown sp							A					
		unknown sp			A									
		unknown sp	A		A									
	COLEOPTERA													
	Staphylinidae	*Philonthus cruentatus* (Gmel.)	A		A									
		Philonthus crotchi Horn	A											
		Tachinus basalis Erichson	A		A									
		Philonthus furvus (Nordm.)												

Table 4. continued

Decomposition Stage	Order and Family	Genus and species	CWH Zone						SBS Zone					
			buried				above ground		buried				above ground	
			immediate		delayed				immediate		disturbed			
			Ex	Pt	Ex	Pt	Ex	Pt	Ex	Pt	Ex	Pt	Ex	Pt
Primary bloat		**Time Since Death**	**2 wks**		**2 wks**		**n/a**		**2 wks**		**n/a**		**n/a**	
	COLEOPTERA													
	Staphylinidae	*Ontholestes cingulatus* (Grav.)			A		-	-			-	-	-	-
		Staphylinini (tribe)					-	-	L		-	-	-	-
	Silphidae	*Nicrophorus defodiens* (Mann.)		A		A	-	-		A	-	-	-	-
		Nicrophorus investigator Zetterstedt		A			-	-		A	-	-	-	-
		Nicrophorus sp					-	-	L		-	-	-	-
	Leiodidae	*Catops basilaris* Say		A	A		-	-	A		-	-	-	-
		Catopocerus cryptophagoides Mann.			A		-	-			-	-	-	-
		Catops sp					-	-	L		-	-	-	-
	Elateridae	*Ctenicera comes* (Brown)			A		-	-			-	-	-	-
		Pyrophorini (tribe)	L		L		-	-			-	-	-	-
	Carabidae	*Pterostichus pumilus* Casey			A		-	-			-	-	-	-
	Histeridae	unknown sp					-	-	L		-	-	-	-
	Family unknown	unknown sp					-	-	L		-	-	-	-
	HYMENOPTERA													
	Pteromalidae	*Nasonia vitripennis* (Walker)	A				-	-		A	-	-	-	-
	Formicidae	*Camponotus herculeanus* (L.)		A		A	-	-		A	-	-	-	-
		unknown sp					-	-		A	-	-	-	-
Secondary bloat		**Time Since Death**	**6 wks**		**6 wks**		**n/a**		**6 wks**		**6 wks**		**n/a**	
	DIPTERA													
	Calliphoridae	*Lucilia illustris* (Meigen)		A			-	-	P	A		A	-	-
		Phormia regina (Meigen)					-	-		A		A		-
		Protophormia terraenovae (Robineau-Desvoidy)					-	-		A		A	-	
		Calliphora vomitoria (L.)					-	-	P	A	P			
		Eucalliphora latifrons (Hough)			P	A	-	-	P		P			
		unknown sp	L				-	-	L		L			
	Muscidae	*Hydrotaea* sp	P	A	P	A	-	-	P	A		A		-
		Ophyra leucostoma (Wied.)		A	P		-	-	P			A		
		Morellia sp	P		P		-	-	P					
		unknown sp	L		L		-	-	L					
		unknown sp	L		L		-	-	L					
	Sphaeroceridae	*Leptocera* sp	A	A		A	-	-		A				

Table 4. continued

Decomposition Stage	Order and Family	Genus and species	CWH Zone						SBS Zone					
			buried				above		buried				above	
			immediate		delayed		ground		immediate		disturbed		ground	
			Es	FS	Es	FS	Es	FS	Es	FS	Es	FS	Es	FS
Secondary bloat		**Time Since Death**	**6 wks**		**6 wks**		**n/a**		**6 wks**		**6 wks**		**n/a**	
	DIPTERA													
	Fanniidae	*Fannia canicularis* (L.)	L P	A	L P	A			L P	A	L	A		
	Phoridae	*Dohrniphora* sp	L	A		A				A		A		
	Piophilidae	*Stearibia nigriceps* (Meigen)								A		A		
	Sarcophagidae	*Boettcheria* sp								A				
		Neobelleria cooleyi (Parker)								A				
	Rhagionidae	unknown sp	L											
	Family unknown	unknown sp			A									
		unknown sp			A				A					
		unknown sp							L		L			
	COLEOPTERA													
	Staphylinidae	*Philonthus cruentatus* (Gmel.)		A		A				A		A		
		Philonthus crotchi Horn		A			-	-	A			A		
		Tachinus basalis Erichson					-	-	A			A		
		Philonthus furvus (Nordm.)					-	-	A		A			
		Staphylinini (tribe)	L				-	-	L					
	Silphidae	*Nicrophorus defodiens* (Mann.)		A	A	A	-	-		A		A	-	-
		Nicrophorus investigator Zetterstedt		A		A	-	-	A		A		-	-
		Nicrophorus sp	L		L		-	-	L		L		-	-
	Leiodidae	*Catops basilaris* Say	A	A	A	A	-	-	A			A	-	-
		Catops sp	L		L		-	-					-	-
	Histeridae	*Hister depurator* Say					-	-		A			-	-
		unknown sp					-	-	L				-	-
	Hydrophiloidae	*Sphaeridium bipustulatum* (F.)					-	-				A	-	-
	Carabidae	*Pterostichus pumilus* Casey					-	-	A				-	-
	Elateridae	Pyrophorini (tribe)	L		L		-	-	L				-	-
	HYMENOPTERA													
	Pteromalidae	*Nasonia vitripennis* (Walker)		A		A	-	-		A			-	-
	Vespidae	*Dolichovespula maculata* (L.)					-	-		A			-	-
		unknown sp					-	-		A		A	-	-
	Formicidae	*Camponotus herculeanus* (L.)	A		A	A	-	-		A		A	-	-
		unknown sp					-	-		A			-	-

Table 4. continued

Decomposition Stage	Order and Family	Genus and species	CWH Zone buried immediate Ex	CWH Zone buried immediate Pt	CWH Zone buried delayed Ex	CWH Zone buried delayed Pt	CWH Zone above ground Ex	CWH Zone above ground Pt	SBS Zone buried immediate Ex	SBS Zone buried immediate Pt	SBS Zone buried disturbed Ex	SBS Zone buried disturbed Pt	SBS Zone above ground Ex	SBS Zone above ground Pt
Active Decay		**Time Since Death**	**3 mo**		**3 mo**		**2 wks**		**3 mo**		**n/a**		**2 wks**	
	DIPTERA													
	Calliphoridae	*Lucilia illustris* (Meigen)		A			L, P				-	-		A
		Phormia regina (Meigen)					L, P	A			-	-	L,P	A
		Protophormia terraenovae (Robineau-Desvoidy)					P				-	-	E	A
		Calliphora vomitoria (L.)							P		-	-		
		unknown sp							L		-	-		
	Muscidae	*Hydrotaea* sp				A			L, P		-	-		A
		Ophyra leucostoma (Wied.)			L, P	A			L, P		-	-		
		Morellia sp							P		-	-		
		unknown sp			L				L		-	-		
		unknown sp			L				L		-	-	L	
	Sphaeroceridae	*Leptocera* sp	P		L, P	A			P		-	-		A
	Fanniidae	*Fannia cannicularis* (L.)	L, P		L, P	A			L, P	A	-	-		A
	Phoridae	*Dohrniphora* sp		A	A						-	-		A
	Heleomyzidae	unknown sp			L				L		-	-		
	Rhagonidae	unknown sp			L						-	-		
	Family unknown	unknown sp							P		-	-		
		unknown sp	L								-	-		
		unknown sp			L				L		-	-		
	COLEOPTERA													
	Staphylinidae	*Philonthus furvus* (Nordm.)		A			A				-	-		A
		Tachinus basalis Erichson	A						A		-	-		A
		Ontholestes cingulatus (Grav.)						A			-	-		A
		Creophilus maxillosus (L.)					A				-	-	A	
		Philonthus cruentatus (Gmel.)		A	A						-	-		A
		Philonthus crotchi Horn									-	-	A	
		Staphylinini (tribe)	L		L		L		L		-	-		
	Silphidae	*Nicrophorus defodiens* (Mann.)		A			A				-	-		A
		Nicrophorus investigator Zetterstedt		A							-	-		
		Thanatophilus lapponicus (Herbst)									-	-		A
		Nicrophorus sp			L						-	-		
	Leiodidae	*Catops basilaris* Say	A	A	A	A		A	A		-	-		A

Table 4. continued.

Decomposition Stage	Order and Family	Genus and species	CWH Zone						SBS Zone					
			buried				above		buried				above	
			immediate		delayed		ground		immediate		delayed		ground	
			Ex	Pr	Ex	Pr	Ex	Pr	Ex	Pr	Ex	Pr	Ex	Pr
Active Decay		**Time Since Death**	**3 mo**		**3 mo**		**2 wks**		**3 mo**		**n/a**		**2 wks**	
	COLEOPTERA													
	Leiodidae	*Catops* sp	L		L				L					
	Cantharidae	*Cantharis* sp.	L		L				L					
	Elateridae	Pyropharini (tribe)	L						L					
	Agyrtidae	*Necrophilus* sp			L									
	HYMENOPTERA													
	Vespidae	*Dolichovespula maculata* (L.)												A
		unknown sp												A
	Formicidae	*Camponotus herculeanus* (L.)				A								A
		unknown sp.	A	A	A									
	Cryptinae	*Atractodes* sp												A
Advanced decay		**Time Since Death**	**11 mo**		**n/a**		**6 wks**		**16 mo**		**n/a**		**n/a**	
	DIPTERA													
	Calliphoridae	*Lucilia illustris* (Meigen)			-	-		A			-			
		Phormia regina (Meigen)			-	-		A			-	-		
	Muscidae	*Ophyra leucostoma* (Wied.)	A		-	-								
		Hydrotaea sp.			-	-		A			-			
		unknown sp.			-	-	L				-	-		
		unknown sp			-	-	L				-	-		-
	Sphaeroceridae	*Leptocera* sp.	PC, A		-	-		A			-	-		
	Fanniidae	*Fannia cannicularis* (L.)	P	P	-	-	P	A			-	-	-	-
	Phoridae	*Dohrniphora* sp.			-	-		A			-	-	-	-
	Piophilidae	*Stearibia nigriceps* (Meigen)			-	-		L, A			-	-	-	-
	Rhagionidae	unknown sp.	L		-	-					-	-	-	-
	Family unknown	unknown sp.			-	-			A		-	-	-	-
		unknown sp.			-	-			L		-	-	-	-
	COLEOPTERA													
	Staphylinidae	*Philonthus furvus* (Nordm.)		A	-	-	A				-	-	-	-
		Tachinus basalis Erichson	A		-	-	A		A		-	-	-	-
		Philonthus crotchi Horn	A		-	-	A				-	-	-	-
		Staphylinini (tribe)			-	-	L				-	-	-	-
	Silphidae	*Nicrophorus defodiens* (Mann.)		A	-	-					-		-	-
	Leiodidae	*Catops basilaris* Say	A	A	-	-	A				-	-	-	-
		Catops sp	L		-	-	L				-	-	-	-

Table 4. continued

			CWH Zone						SBS Zone					
			buried				above		buried				above	
Decomposition Stage	Order and Family	Genus and species	immediate		delayed		ground		immediate		disturbed		ground	
			Ex	Pt	Ex	Pt	Ex	Pt	Ex	Pt	Ex	Pt	Ex	Pt
Advanced decay		**Time Since Death**	**11 mo**		**n/a**		**6 wks**		**16 mo**		**n/a**		**n/a**	
	COLEOPTERA													
	Hydrophiloidae	*Sphaeridium bipustulatum* (F.)			-	-	Λ				-	-	-	-
	Histeridae	unknown sp.	L		-	-					-	-	-	-
	Elateridae	*Ctenicera comes* (Brown)			-	-	Λ				-	-	-	-
		Pyropharini (tribe)	L		-	-	L				-	-	-	-
	Agyrtidae	*Necrophilus* sp.			-	-		L			-	-	-	-
	HYMENOPTERA													
	Pteromalidae	*Nasonia vitripennis* (Walker)			-	-		Λ			-	-	-	-
	Formicidae	*Camponotus herculeanus* (L.)			-	-		Λ			-	-	-	-
		unknown sp.			-	-		Λ			-	-	-	-
Dry/Remains		**Time Since Death**	**n/a**		**n/a**		**3 mo**		**n/a**		**n/a**		**n/a**	
	DIPTERA													
	Muscidae	*Hydrotaea* sp.	-	-	-	-		Λ	-	-	-	-	-	-
		unknown sp.	-	-	-	-	L		-	-	-	-	-	-
	Sphaeroceridae	*Leptocera* sp.	-	-	-	-	P	Λ	-	-	-	-	-	-
	Fanniidae	*Fannia cannicularis* (L.)	-	-	-	-	P	P	-	-	-	-	-	-
	Piophilidae	unknown sp.	-	-	-	-		L	-	-	-	-	-	-
	COLEOPTERA													
	Staphylinidae	*Philonthus cruentatus* (Gmel.)	-	-	-	-	Λ		-	-	-	-	-	-
		staphylinini (tribe)	-	-	-	-		L	-	-	-	-	-	-
	Silphidae	*Nicrophorus defodiens* (Mann.)	-	-	-	-		Λ	-	-	-	-	-	-
		Nicrophorus investigator Zetterstedt	-	-	-	-		Λ	-	-	-	-	-	-
	Histeridae	unknown sp.	-	-	-	-		L	-	-	-	-	-	-

The buried carcasses did not reach the active decay stage until 3 months after death, but the above-ground carcasses had reached this stage by 2 weeks after death (Table 2). *Phormia regina* and *Protophormia terraenovae* (Robineau-Desvoidy) immatures (Table 4) were found in large masses on the above-ground carcasses in both zones. *L. illustris* larvae and pupae were collected only from above-ground carcasses in the CWH zone, although adult *L. illustris* were collected from pitfall traps above buried pigs in the CWH zone and beside above-ground carcasses in the SBS zone. I collected adult *Hydrotaea* sp., *Leptocera* sp. (Sphaeroceridae), *Dohrniphora* sp. and *Fannia cannicularis* in pitfall traps beside above-ground pigs in the SBS zone. Staphylinidae and Silphidae were collected from above-ground carcasses and pitfall traps in both zones. I collected adult *Catops basilaris* Say (Leiodidae) and larval Staphylinidae from pitfall traps and above-ground carcasses in the CWH zone.

Leptocera sp., whose pupal cases closely resemble those of the Piophilidae, were collected as pupae on buried carcasses in both zones at 3 months after death, during the active decay stage (Table 4). I collected Heleomyzidae larvae from buried carcasses in the SBS zone. I did not observe maggot masses on any of the buried carcasses in either zone.

Buried carcasses in the CWH zone had entered advanced decay by 11 months after death and were still in this stage at 16 months after death (Table 2). Buried carcasses in the SBS zone were also in this stage when I exhumed them at 16 months after death (Table 2). I collected very few insects on buried carrion at this time.

However, larval Histeridae were collected from buried carcasses at this point (Table 4).

Above-ground carcasses in the CWH zone had entered the advanced decay stage by 6 weeks after death (Table 2). Adult *Leptocera* sp., *Sphaeridium bipustulatum* (F.) and *Ctenicera comes* (Brown) (Elateridae) were collected from the above-ground carcasses and pitfall traps, as well as adult and immature *F. canicularis* and *Stearibia nigriceps* (Meigen) (Piophilidae). I also collected larval *Necrophilus sp.* (Argyrtidae) from above-ground carcasses. Since the above-ground carcasses in the SBS zone were eaten by a large scavenger, no further data were available.

By 3 months after death, above-ground carcasses in the CWH zone had entered the dry/remains stage (Table 2). Larval and adult *Leptocera* sp. were collected on the above-ground carcasses (Table 4). This was the first time that I collected larvae of this species on above-ground carcasses. Throughout the study, I observed the ant *Camponotus herculeanus* and silphids *Nicrophorus defodiens* Mannerheim and *Nicrophorus investigator* Zetterstedt feeding on carcasses.

2.5.2 Immediate *vs.* delayed burial

Immediately buried carcasses and carcasses buried 48 h after death all went through the decompositional stages at the same rate, with no measurable differences between the two treatments (Table 2). However, I observed some differences in insect succession. Although blowfly adults of various species were collected in pitfall traps above carcasses from both treatments, I collected only prepupal larvae of *L. illustris* on the delayed burial carcasses (Table 4) By 6 weeks after death I collected pupae of the blowfly species *E. latifrons* and the muscid species *O. leucostoma* from carcasses buried 48 h after death, but not from immediately buried carcasses (Table 4). At 3 months after death I collected immature Heleomyzidae and *Necrophilus* sp. from the delayed burial but not the immediately buried carcasses (Table 4). The study of carcasses buried 48 h after death was terminated at this point.

2.5.3 Immediate *vs.* disturbed burial

I observed differences in the presence of larval Calliphoridae and Muscidae between the two treatments at 6 wk after death. Pupae of the blowfly *L. illustris* and the muscids *Hydrotaea* sp., *O. leucostoma* and *Morellia* sp. were collected from the undisturbed carcasses, but were not present on carcasses in the disturbed treatment (Table 4). However, I collected pupae of *L. illustris* on these carcasses when they were originally exhumed at 2 weeks after death (Table 4). *Leptocera* sp., *Boettcheria* sp. (Sarcophagidae) and *Neobelleria cooleyi* (Parker) adults were collected in pitfall traps above the undisturbed carcasses but not in pitfall traps above the disturbed carcasses. The Coleopteran family Histeridae was represented in both treatments with *Hister dispurator* Say present on undisturbed carcasses and *S. bipustulatum* present only on disturbed carcasses. Larval Histeridae were present only on the undisturbed carcasses (Table 4).

3. DISCUSSION

3.1 DIVERSITY IN EPHEMERAL HABITATS

Ephemeral habitats, such as carrion and dung are often very rich in species In order for these insect species to survive, they must be mobile enough to colonize empty habitats rapidly, in order to compensate for local population extinctions (Hanski 1987) The higher species richness on buried than above-ground carrion (Figure 6) contradicts the findings of Smith (1986) and Leclercq (1969) In contrast, the greater evenness between species on buried than above-ground carrion is supported by other authors (Leclercq 1969, Smith 1986)

Competition for resources could explain the low diversity of insect species on above-ground carcasses The carcasses were completely consumed, a frequent occurrence for both carrion and dung This has been observed to result in reductions in larval, pupal and adult blowfly size (Hanski 1986, Hanski 1986) Colonization by tens or hundreds of species may occur (Payne 1965, Hanski 1986, Anderson and VanLaerhoven 1996) The predominance of Calliphoridae larvae on above-ground carcasses (Figure 7) suggests that competition for resources by blowfly maggot masses may have prevented other species from establishing It is also possible that I missed collecting some dipteran species due to the overwhelming abundance of a few species within the maggot masses on above-ground carcasses On buried carcasses, there were no such maggot masses and little apparent competition by the few insects present

As postulated in the equilibrium theory of island biogeography (MacArthur and Wilson 1972), species richness should be highest in large carrion habitats which are near other similar habitats and lowest in small, isolated habitats (Hanski 1987, Hewadikaram and Goff 1991) Because the carcasses in this study were all the same size, burial of a carcass would have been equivalent to increasing the distance a colonizing insect had to travel to reach it However, in contrast to the theory, the species richness was greatest in the buried carcasses (Figure 7, Table 3), possibly due to competition in the above-ground carcasses precluding the successful colonization by more species

Differences in species composition between the CWH and SBS zones (Figure 9) may reflect differences in the range of carrion-inhabiting species However, the characteristics of the soil would also have influenced which species were present in the soil and available to colonize buried carcasses In addition, the physical characteristics of the soil after digging would determine which non-soil dwelling species could reach the buried carrion (Kevan 1968) The presence of immature *Calliphora vomitoria* and *Lucilia illustris* on buried carcasses at the two week exhumation in the SBS zone and *Lucilia illustris* immatures only on carcasses buried after 48 h in the CWH zone at the same time period (Table 4) was likely due to differences in soil composition The soil in the SBS zone site was predominately clay which formed large coarse fragments after excavation, allowing easier access to the buried carcasses *Calliphora* and *Lucilia* spp (Table 4) (Fuller 1932) and species in the family Phoridae (Lundt 1964, Nuorteva 1977), e g *Dohrniphora* sp (Table 4) are capable of burrowing (Lord *et al* 1992) Nuorteva's (1977) statement that the presence of blowfly and Piophilidae larvae on a buried body indicated that the body was kept unburied for a portion of time was evidently erroneous

However, an alternative explanation is also possible It rained during the placement of carcasses in the CWH zone, preventing any fly activity In the SBS zone, it was warm and sunny during the 8 h it took to bury all the carcasses Some blowflies could have been attracted to the carcasses and oviposited before burial, but the presence of younger instars still indicates that some penetrated the soil to reach the carcasses

The rapid development of insects on the above-ground carcasses during the early stages of decay (Table 4) was undoubtedly influenced by action of maggot masses which can increase the internal temperature of a carcass up to 40 °C, although this fluctuates considerably during a 24 h period (Anderson and VanLaerhoven 1996) Because soil acts as a temperature sink, there was much less fluctuation in temperature within the soil than in ambient air temperature (Figure 3) as also observed in other studies, especially as depth within the soil increases (Kevan 1968, Wallwork 1970, Wallwork 1976, Rodriguez and Bass 1985) The resulting consistently cooler temperatures than in above-ground carcasses would have retarded the development of carrion-inhabiting insects Any differential effects of low (CWH) and freezing (SBS) temperatures during the winter were not evident in this study, despite a slight difference in the rate of decomposition due to the winter soil conditions in the SBS zone

The slower decomposition of buried than above-ground carcasses (Table 2) has also been observed in other studies (Lundt 1964, Payne 1965, Payne *et al* 1968) The rate of decomposition of buried carcasses in both biogeoclimatic zones was much slower than in South Carolina (Payne *et al* 1968) The slow rate of decomposition of buried carrion explains the similarity of the communities of insects collected at 3, 11 and 16 months after death in the CWH zone (Figure 9)

3.2 SUCCESSION

3.2.1 Immediately buried carcasses

3.2.1.1 Dipteran carrion fauna

Numerous species of Diptera were predictably the most common inhabitants of buried carcasses in this study The collection of immature *Fannia canicularis* on buried carcasses in both biogeoclimatic zones (Table 4) is consistent with the common occurrence of this species in the soil (Peterson 1951), as well as on carrion in later stages of succession (Anderson and VanLaerhoven 1996) Its early role in the succession on buried carrion is possibly due to the moisture associated with buried carcasses, since this species prefers moist habitat (Smith 1986)

The sequence in the SBS zone of *Calliphora vomitoria* larvae and pupae during primary bloat (2 weeks after death), then *Hydrotaea* sp , *Morellia* sp and *Ophyra leucostoma* pupae during secondary bloat (6 weeks after death) follows a similar successional pattern to that found by Megnin (1894), who found a succession of insects on buried carrion that began with *C. vomitoria* and *Muscina stabulans* soon after death, followed by *Ophyra anthrax* *O. leucostoma* were also collected from dog cadavers buried in coffins at 2 months after death in Washington, D C (Motter 1898) In British Columbia, immature *Hydrotaea* sp were collected from 5 days to 10 months after death on buried human bodies (Anderson 1995) Muscids have previously been collected from buried carrion, but their time of colonization was not known (Lundt 1964, Nuorteva 1977) My collection of *Neobelleria cooleyi* (Sarcophagidae) adults in pitfall traps above buried carcasses in the primary bloat stage, in the SBS zone 2 weeks after death agrees with the finding of this species on buried human bodies 20 days after death in the Prince George Forest Region (Anderson 1995)

In the only experimental study that used buried human cadavers, Calliphoridae and Sarcophagidae were collected from the cadavers but were identified only to the family level (Rodriguez and Bass 1985) Other studies have been done on human bodies exhumed from actual homicide cases, or from anthropological studies (Megnin 1894, Motter 1898, Lundt 1964, Gilbert and Bass 1967, Leclercq 1969, Stafford 1971, Nuorteva 1977, Lord *et al* 1992) The study by Rodriguez and Bass (1985) utilized six cadavers each buried at a different time of year Unfortunately this work suffered from many problems, including no above-ground controls, no replication, two cadavers with missing brains and internal organs that would have eliminated bloat-causing gut fauna, burial at different times after death, some bodies clothed and others not clothed which can influence insect succession (Dillon and Anderson [illegible]), burial at different depths and only [illegible] m apart, too close for insects to distinguish them as separate, proximity of many other bodies, and repeated exhumation and re-burial.

My collection of adult *Leptocera* sp. (Sphaeroceridae) and *Dohrniphora* sp. (Phoridae) in pitfall traps above bloated buried carcasses in both zones and the recovery of larval *Dohrniphora* sp. from buried carcasses during secondary bloat in the CWH zone and pupal of *Leptocera* sp. from buried carcasses during the active stage in both zones (Table 4) agrees with the results of Payne (1968) who collected adult *Leptocera* sp. and *Dohrniphora incisuralis* (Loew) during the bloat stage and larvae of these two species at the onset of the active stage in North Carolina. Motter (1898) stated that Phoridae colonized buried dog carrion at 2 months after death, but Megnin (1894) did not find *Phora aterrima* on buried carrion until a year after death. Nuorteva (1977) and Lundt (1964) noted the presence of Phoridae on buried bodies, but did not indicate a time of colonization. The occurrence of larval Heleomyzidae on buried carcasses in the SBS zone during the active decay stage, at 3 months after death (Table 4) is in agreement with Lundt's (1964) documentation of heleomyzids on buried carrion.

3.2.1.2 *Coleopteran carrion fauna*

Staphylinidae beetles are commonly found on buried carrion (Lundt 1964 Nuorteva 1977, Rodriguez and Bass 1985) In the Vancouver, Cariboo and Prince Rupert Forest Regions of British Columbia, various species of Staphylinidae were collected from buried human bodies from 5 days to 5 months after death (Anderson 1995) They were the predominant beetles collected on buried carrion in both zones throughout the 16 month period (Table 4) I found adult *Philonthus* sp at primary bloat, much earlier than observed by Megnin (1894), who stated that *Philonthus ebeninus* did not arrive on buried bodies until two years after death in France In North Carolina, Staphylinidae were not present on buried pigs until the active stage (Payne *et al* 1968), also later than in my study Other prominent beetles were the silphids *Nicrophorus defodiens* and *Nicrophorus investigator* (Table 4) I initially collected them from buried carcasses during the primary bloat stage, in both zones These results contradict a previous report that silphids could not locate carrion buried under 4 cm of sand (Shubeck 1985)

3.2.1.3 *Hymenopteran carrion fauna*

The carpenter ant *Camponotus herculeanus* was the most common hymenopteran I collected It occurred during the primary bloat stage, on buried carcasses in both biogeoclimatic zones (Table 4) In North Carolina, Payne *et al* (1968) collected other ant species during the fresh and bloat stages from a pig carcass in a simulated coffin. Perpetrators rarely bury homicide victims in coffins and this scenario would influence the ability of insects to reach the carcass.

3.2.2 Carcasses buried after 48 hours

It has often been assumed that the presence of blowfly larvae, pupae or pupal cases indicates that a body has remained above ground for a period of time prior to burial (Gilbert and Bass 1967, Nuorteva 1977, Vanezis *et al.* 1978, Heath 1982). This assumption is contradicted by published evidence (Lord *et al.* 1992), as well as data from this study (Table 4). Nuorteva (1977) stated that the presence of Histeridae indicated that the body was left unburied for at least 2-3 days and that the presence of Piophilidae indicated that the body was left unburied for at least a week. However I collected *Hister dispurator* adults and histerid larvae from immediately buried carcasses in the SBS zone. I did not collect piophilid larvae from immediately buried carcasses, but adults were caught in pitfall traps above immediately buried carcasses in the SBS zone, implying that they were attracted to the buried remains. It is possible that immature Piophilidae larvae were not collected from buried carcasses in this experiment due to the conversion of fatty tissue into adipocere, removing the favored food of Piophilidae (Smith 1986). Thus, none of my results can be used to indicate conclusively whether or not delayed burial has occurred.

3.2.3 Disturbed burial

Similarly, there was no evidence that exhumation and re-burial allowed colonization by species not typically found on buried carcasses or that it gave species that were incapable of penetrating 30 cm of soil a chance to reach a buried carcass However, my study is hampered by small sample size In the United States, times of disturbance as well as elapsed time since death have been determined using insect evidence (Anderson pers com) Since this effect is likely to be site specific, it is important to be aware of this possibility More research is required to determine under what ecological conditions this effect may be observed

3.3 Ecological Roles of Carrion Fauna

During heterotrophic succession, entomophagous insects tend to increase as the succession continues (Mohr 1943, Payne 1965) The most common predators in the soil are beetles in the families Carabidae and Staphylinidae (Kevan 1968, Wallwork 1976) Although the great majority of insects collected in this study were saprophagous, generalist predatory carabid, histerid and staphylinid beetles, as well as ants and wasps were well represented on both above-ground and buried carcasses in both zones, probably feeding on dipteran eggs and larvae I also collected elaterid beetles but this family has both carnivorous and saprophytic members (Kevan 1968, Wallwork 1976). Predaceous dipteran larvae, *Ophyra leucostoma* and *Hydrotaea* sp were collected on buried carcasses, the former in the SBS zone and the latter in both zones *Nasonia vitripennis* and *Atractodes* sp , both parasitoids of immature dipterans, were attracted to both above-ground and buried carcasses

3.4 FORENSIC IMPLICATIONS

3.4.1 Elapsed Time Since Death

The major use of forensic entomology has been to determine elapsed time since death The elapsed time since death can be used to confirm or refute a suspect's alibi and to aid in the identification of unknown victims by focusing an investigation into the correct time frame This information can be vital in a homicide investigation (Anderson and VanLaerhoven 1996)

There are two methods of determining elapsed time since death using insect evidence (Goff 1993) The first uses maggot age and developmental rates Since blowflies usually arrive and begin laying eggs within minutes after death (Anderson and VanLaerhoven 1996), an analysis of the oldest insects present will give a minimum post-mortem interval This requires accurate collection of the oldest insects and accurate temperature records The second method uses the succession of insects on a decomposing corpse An entomologist can predict a window of time in which death occurred by analyzing the presence and absence of species on a body Although some species may no longer be present, pupal cases can indicate a minimum post mortem interval This method requires an accurate database of insect succession My results show that insect succession differs between above-ground and buried carcasses and between biogeoclimatic zones in B.C., indicating that databases for particular zones and scenarios must be established before entomological evidence can be used accurately.

3.4.2 Temperature

In the case of a crime scene, the temperature of the body prior to discovery must be predicted in order to determine the minimum post-mortem interval using maggot developmental rates. This is usually done by comparing temperature data taken at the scene, with data from the nearest weather station during the same time period. If there is a good correlation between the two, then the weather station data can be used to predict what the temperature at the scene was prior to discovery of the body. This technique assumes that there is a good correlation between the ambient temperature at the scene and the internal temperature of the body. In my study, there was a poor correlation between the weather station ambient air temperature and the internal temperature of above-ground carcasses in the CWH zone (Table 1), probably due to maggot mass activity raising the internal carcass temperature and for micrometeorological differences between the weather station and the research sites. Support for these causes are found in the excellent correlation between ambient air and internal above-ground carcass temperature in the SBS zone (Table 1) before maggot mass activity raised the internal carcass temperature and when the two temperatures were recorded within 1 m of each other. Since there were no maggot masses on any of the buried bodies, it is not surprising that ambient air temperature was well correlated (Table 1) with internal buried carcass temperature, at least during the spring, summer and fall in the SBS zone. During the winter in the SBS zone, ambient air temperature continued to fluctuate, but internal temperature of the buried carcass in the frozen ground did not, resulting in no correlation (Table 1).

Because soil temperature was the best predictor of internal buried carcass temperature (Table 1), it would be best to establish soil temperatures at scenes of buried victims. The strong relationship between soil and weather station temperatures in the CWH zone (Table 1) indicates that soil temperature can be correlated with weather station temperature data after discovery of a buried cadaver. Soil temperature has been used in at least one case, to determine blowfly development rates (Lord *et al* 1992).

3.4.3 Indicator species

The occurrence of certain species of insects on buried carcasses at predictable times in the succession suggests that these species can be used as indicators of the elapsed time since death of a buried homicide victim.

3.4.3.1 ***Family Calliphoridae***

The developmental rates of calliphorid flies are known for a variety of temperatures (Nuorteva 1977, Greenberg 1993) making them extremely useful indicators of the post-mortem interval. Third instar larvae of *Calliphora vomitoria* and *Lucilia illustris* were present by the exhumation at 2 weeks after death in the SBS zone Using the soil temperature and the stage of development, it is possible to determine how long it took these flies to reach third instar, which was the oldest stage collected at 2 weeks after death Using Greenberg's developmental data for *C. vomitoria* at 12 5°C (1993), death occured on or before 15 June 1997 Using Nuorteva's developmental data for *L. illustris* at 15°C (1977), death occured on or before 16 June 1997 Because both these estimates use a temperature higher than was actually found at the scene (mean internal buried carcass temperature of 11 6°C), death must have occured earlier than 15 June 1997 This is a conservative estimate because this assumes that the larvae had just entered third instar, when in actuality, they likely had been in that stage for a few days The actual date of death was 10 June 1997

In the CWH zone, prepupal *L. illustris* were collected from carcasses buried 48 hours after death Using the soil temperature and the stage of development, it is possible to determine how long it took these flies to reach the prepupal stage, which was the oldest stage collected at 2 weeks after death Using Nuorteva's developmental data for *L. illustris* at 15°C (1977), death occured on or before 21 June 1997 Because this estimate uses a temperature higher than was actually found at the scene (mean internal buried carcass temperature of 12 2°C), death must have occured earlier than 21 June 1997 This is a conservative estimate because this assumes that the larvae had just entered the prepupal, when in actuality, they could had been in that stage for a few days The actual date of death was 17 June 1997

3.4.3.2 Family Muscidae

The family Muscidae contains some potential indicator species that could be used to calculate the elapsed time since death. At 6 weeks after death, pupal *Hydrotaea* sp. and *Morellia* sp. were collected from buried carcasses in both zones, and pupal *Ophyra leucostoma* were collected from buried carcasses in the SBS zone (Table 4). If the developmental rates for these three muscids were known at particular temperatures, the time taken for immatures to reach the pupal stage could be calculated, thus giving a minimum post-mortem interval.

3.4.3.3 Family Fanniidae

Fanniid flies are usually considered to colonize cadavers late in the succession of insect species. However, pupal *Fannia canicularis* were collected from buried carcasses at 2 weeks after death in the SBS zone and larval and pupal *F. canicularis* were collected from buried carcasses at 6 weeks after death in the CWH zone, possibly due to the wet condition of the buried carcasses which is preferred by members of this family. Therefore, when using this species to predict a minimum post-mortem interval, it is important to note its early arrival on buried carrion, as well as the difference in arrival times between the two zones.

3.4.3.4 Family Phoridae

Larvae of *Dohrniphora* sp were collected on buried carcasses in the CWH zone at 6 weeks after death The presence of immatures of this species gives a minimum post-mortem interval of > 2 weeks after death and < 6 weeks after death

3.4.3.5 Family Sphaeroceridae

Pupae of *Leptocera* sp were collected on buried carcasses in both zones at 3 months after death The presence of immatures of this species gives a minimum post-mortem interval of > 6 weeks after death and < 3 months after death Pupal cases of *Leptocera* sp were collected on buried carcasses in the CWH zone at 11 months after death The presence of pupal cases of this species gives a minimum post-mortem interval of > 3 months and < 11 months after death

3.4.3.6 Family Heleomyzidae

Larvae of this family were collected on buried carcasses in the SBS zone and on carcasses buried after 48 hours in the CWH zone at 3 months after death (Table 4) This family is also a later successional species, since the presence of immatures gives a minimum post-mortem interval between 6 weeks and 3 months after death

3.4.3.7 Coleopteran Families

Since most of the coleopteran species collected on the buried carcasses are general predators, they cannot be used to determine a post-mortem interval

3.4.4 Recommendations

1. When using the succession of insect species to determine the elapsed time since death of a buried homicide victim, it is important to have a database of insect succession for that particular ecosystem Therefore ideally, a successional database for each major biogeoclimatic zone should be established
2. Since dipteran species other than those from the family Calliphoridae could be used as indicator species, more studies on the developmental rates of these species would allow the estimation of a more precise post-mortem interval
3. When using the developmental rates of early successional dipteran species to determine the elapsed time since death of a buried homicide victim, a datalogger should be placed in the soil for comparison to the nearest weather station If the weather station records soil temperature, this should be used instead of ambient air temperature
4. Since disturbance can potentially change the succession of insect species on a buried homicide victim, more research should be done to determine under what ecological conditions this effect may arise and how to determine when this disturbance has occurred
5. Although depth of burial was not examined in this study, it probably affects the succession of insect species on the carcasses Therefore, more research should be done to determine how the depth of burial influences insect succession

6. Because no maggot masses were observed on any buried carcass, the presence of maggot masses, large numbers of blowfly pupae or blowfly pupal cases on a buried homicide victim is a probable indicator that the body was not buried immediately. This is a possible indication that the crime scene and the death scene are not the same, therefore investigators should determine where the body was after death, but prior to burial

4. REFERENCES

Anderson, G S. Assistant Professor, School of Criminology, Simon Fraser University, Burnaby , B C., personal communication.

Anderson, G. S 1995. The use of insects in death investigations. an analysis of, forensic entomology in British Columbia over a five year period Can. Soc Forensic Sci. J. 28 (4). 277-292.

Anderson, G. S. and S. L. VanLaerhoven. 1996. Initial studies on insect succession on carrion in southwestern British Columbia. J. Forensic Sci. 41 (4). 617-625.

Catts, E P and M. L. Goff 1992 Forensic entomology in criminal investigations Ann. Rev. Entomol. 37: 253-272.

Denno, R F and W R Cothran 1976. Competitive interaction and ecological strategies of sarcophagid and calliphorid flies inhabiting rabbit carrion Ann Entomol. Soc Am 69. 109-113.

Dillon, L C. 1997 Insect succession on carrion in 3 biogeoclimatic zones of B C. Dept. of Biological Sciences, Simon Fraser University M Sc thesis.

Dillon, L C and G S Anderson 1995. Forensic Entomology The use of insects in death investigations to determine elapsed time since death Canadian Police Research Centre. Rep. No. TR-05-95.

Fuller, M E 1932. The effect of carcass burial on blowflies J Coun. Sci Ind Res 5 162-164

Gilbert, B M and W M Bass 1967. Seasonal dating of burials from the presence of fly pupae Am Antiquity 32 534-535

Goddard, J and P K Lago 1985. Notes on blowfly (Diptera Calliphoridae) succesion on carrion in Northern Mississippi. J Entomol. Sci 20 312-317

Goff, M L. 1991. Comparison of insect species associated with decomposing remains recovered inside dwellings and outdoors on the island of Oahu, Hawaii J Forensic Sci 36 748-753.

Goff, M L. 1993. Estimation of Postmortem interval using arthropod development and successional patterns Forensic Sci Rev. 5 81-94

Goff, M L and M M Flynn 1991 Determination of postmortem interval by arthropod succession a case study from the Hawaiian islands J Forensic Sci 36 607-614

Goff, M L and C B Odom 1987 Forensic entomology in the Hawaiian Islands, U S A Three case studies Am J Foren Med Path 8 45-50

Goff, M L , C B Odum and M Early 1986 Estimation of postmortem interval by entomological techniques a case study from Oahu, Hawaii Bull Soc Vector Ecol 11 242-246

Goff, M L , A I Omori and K Gunatilake 1988 Estimation of postmortem interval by arthropod succession Three case studies from the Hawaiian Islands Am J Foren Med Path 9 220-225

Greenberg, B 1993 Different developmental strategies in two boreal blow flies (Diptera Calliphoridae) J Med Entomol 3 (2) 481-484

Greenberg, B 1985 Forensic entomology case studies Bull Entomol Soc Am 31 (4) 25-28

Hanski, I 1987 Colonization of ephemeral habitats, *IN* Colonization, succession and stability A J Gray *et al.* Ed British Ecological Society, Oxford pp 155-186

Hanski, I 1986 Nutritional ecology of dung- and carrion-feeding insects , *IN* Nutritional ecology of insects, mites, spiders and related invertebrates F Slansky and J G Rodriguez Ed John Wiley, New York pp 837-885

Heath, A C G 1982 Beneficial aspects of blow flies New Zealand Entomol 7 (3) 343-348

Hewadikaram, K and M Goff 1991 Effect of carcass size on rate of decomposition and arthropod succession patterns Am J For Med Path 12 235-240 .

Kevan, D K M 1968 Soil animals H F & G Witherby, London

Krebs, C J 1989 Ecological methodology Harper & Row, New York

Leclercq, M 1969 Entomolgical parasitology entomology and legal medicine Pergamon Press, Oxford

Lord, W D , T R Adkins and E P Catts 1992 The use of *Synthesiomyia nudesita* (Van Der Wulp (Diptera Muscidae) and *Calliphora vicina* (Robineau-Desvoidy) (Diptera Calliphoridae) to estimate the time of death of a body buried under a house J Agric Entomol 9 (4) 227-235

Lundt, H 1964 Ecological observations about the invasion of insects into carcasses buried in soil Pedobiologia 4 158

MacArthur, R H and E O Wilson 1972 The theory of island biogeography. Princeton University Press, Princeton, N J

Megnin, P. 1894. Faune des cadavres application de l' entomologie a la medicine legale Encyclopedie Sci Aide- Memoire, Paris

Meidinger, D and J Pojar 1991 Ecosystems of British Columbia British Columbia Ministry of Forests

Microsoft 1985 Microsoft Excel, 5 0 Microsoft Corporation

Minitab 1994 10 1 Minitab Inc , 3081 Enterprise Drive, State College, PA 16801-3008

Mohr, C O 1943 Cattle droppings as ecological units Ecol Monogr 13 275-309

Motter, M G 1898 A contribution to the study of the fauna of the grave - a study of 150 disinterments, with some additional observations J N Y Entomol Soc 6 201-231

Nuorteva, P 1977 Sarcosaprophagous insects as forensic indicators, *IN* Forensic medicine a study in trauma and environmental hazards C G Tedeschi Ed Saunders, New York pp 1072-1095

Payne, J A 1965 A summer carrion study of the baby pig *Sus Scrofa* L Ecology 46 592-602

Payne, J A , E W King and G Beinhart 1968 Arthropod succession and decomposition of buried pigs Nature 219 1180-1181

Peterson, A 1951 Larvae of insects Part II Lithoprint Edwards, Ann Arbor, Michigan

Reed, H B 1958 A study of dog carcass communities in Tennessee with special reference to the insects Am Mid Nat 59 213-245

Rodriguez, W C and W M Bass 1985 Decomposition of buried bodies and methods that may aid in their location J Forensic Sci 30 836-852

Shubeck, P P 1985 Orientation of carrion beetles to carrion buried under shallow layers of sand (Coleoptera Silphidae) Entomol News 96 163-[illegible]

Skinner, M and R A Lazenby 1983 Found! Human Remains. Archeology Press, Simon Fraser University, Burnaby, B.C.

Smith, K G V 1986. A manual of forensic entomology British Musem (Nat. Hist.) London, and Cornell University Press Ithaca, N.Y

Spitz, W U and R S Fisher 1973. Medicolegal investigation of death. Charles C Thomas, Springfield, Illinois.

Stafford, F 1971. Insects of a medieval burial. Sci. and Anth. 7: 6-10.

Vanezis, P., B G. Sims and J. H Grant. 1978 Medical and scientific investigations of an exhumation in unhallowed ground Med. Sci. Law 18: 209-221

Wallwork, J A 1976 The distribution and diverstiy of soil fauna. Academic Press, New York

Wallwork, J A 1970 Ecology of soil animals McGraw-Hill, London.