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Initial Studies on Insect Succession on Carrion in Southwestern British Columbia

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ABSTRACT: This is the first report of an ongoing study of insect succession on carrion in British Columbia. Pig (*Sus scrofa* L.) carcasses were used as human models to determine insect succession on carrion over time in an open, sunlit, rural area in summer in southwestern British Columbia, in order to begin a database of insect colonization of carrion in this province. Insects colonized the remains in sequence over 271 days postmortem. Some species, in particular, those in the Piophilidae and Dermestidae families, were collected earlier in the decomposition process than usually reported from other regions, probably indicating geographic variation in colonization times. Maggot activity raised internal carcass temperature, but minimum and maximum internal temperatures fluctuated more than ambient temperatures, with diel internal temperature differences of more than 35°C. Soil fauna also showed considerable changes in identity and number of species, and had not returned to pre-carcass levels 271 days postmortem.

KEYWORDS: forensic science, forensic entomology, insect succession, carrion ecology, British Columbia, Canada

In a death investigation, determining time of death is of paramount importance. Medical parameters can be used to determine time of death in cases in which death has taken place shortly before discovery (1,2), but this becomes much more difficult as time progresses. After 72 h, forensic entomology is usually the most accurate and often the only method for determining time of death (3). In many homicide cases, the body is often dumped, or the victim was killed in a remote area, delaying discovery. This means that, in many cases, homicide victims are not discovered until days, or even months or more after death, and it is in these cases that determining time of death may be most vital.

Forensic, or medicolegal entomology is the study of insects associated with carrion in order to determine the time of death. Insects are often the first arrivals at a death scene and they arrive in a predictable sequence. A carcass, whether human or animal, goes through a large series of biological, chemical, and physical changes as it decomposes from the fresh to the skeletal state. Different stages of this decomposition process are attractive to different species of insects. The carcass is a temporary, rapidly changing resource which supports a large, dynamic arthropod community. When the sequence of insects colonizing carrion is known, an analysis of the arthropod fauna on a carcass can be used to determine the time of death. This procedure can provide accurate and precise methods for estimating elapsed time since death and is used in many homicide investigations worldwide (4,5).

The species of insects associated with carrion, and their times of colonization, vary with geographic region, based on many parameters, so it is important that a database be established for all regions in which forensic entomology is used. Carrion communities have been studied in several temperate and tropical regions worldwide (6–19), but no such studies have been conducted in British Columbia, nor published in Canada since 1897 (20). The objective of this work was to begin a database of insect succession on carrion in British Columbia.

Methods and Materials

A rural, farming area in the Fraser Valley Region of British Columbia was chosen as the research site. This area, in the southwest of the province, approximately 80 km (50 miles) east of Vancouver, is in the Coastal Western Hemlock biogeoclimatic zone, which includes the majority of the coastal region of British Columbia from the border of Washington State, north to Alaska, Vancouver Island, the Gulf Islands and the Queen Charlotte Islands.[2] The study area consisted of open fields with both coniferous and deciduous trees in the vicinity. Seven research sites were chosen. Each site was in an open, sunlit area. The ground cover was primarily grass pasture. The sites were a minimum of 50 m apart so that olfactory orientation by insects to each carcass was independent.

Seven 22 kg (50 lb) pigs (*Sus scrofa* L.) were used as models for human decomposition. The pigs were killed at the research site on 9 June 1992, by a single shot to the back of head from a .22 caliber handgun to mimic common homicide scenarios. After death, each carcass was shot a second time in the thorax. Each carcass was placed immediately at its study site, so that no time elapsed between death and exposure to insects. The study methods were approved by the Canadian Council on Animal Care. The date of death was designated as day 0.

At each site, the carcass was protected from large animal scavenging by a cage. The cages were 100 × 70 × 45 cm, and were constructed with 2.5 cm diameter plumbers' PVC piping, covered with 2.5 cm mesh hardware cloth. Hardware cloth also was secured to the ground surrounding the cage for 30 cm to prevent animals from digging under the cages. Grass rapidly grew through the

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mesh and secured it firmly to the ground. The cages were staked to the ground, and were removable for easy access.

The carcasses were divided into three groups. Group 1 consisted of three carcasses. Each carcass was placed directly on the ground, the most common situation in which decomposed remains of homicide victims are found. These carcasses were examined for insect activity immediately after death, then every day for 22 days, then every 2 to 3 days until 3.5 months after death, then at less frequent intervals until no further insect evidence was recorded (9.5 months after death). At each examination time, insects and other arthropods were sampled from on, in, under and around the carcasses, as would occur in a normal homicide situation in which forensic entomology is utilized. Insects were returned to the lab and either killed, labeled and identified or raised to adulthood for later identification. Some specimens were identified at Biosystematics Research Centre, Ottawa.

Group 2 consisted of two carcasses. Before these carcasses were placed at their sites, a 250 mL soil sample was taken from the area for later lab analysis, to determine the original soil fauna prior to carcass placement. The carcasses were then placed at their decomposition sites on mesh platforms to allow them to be lifted and weighed. The platforms were made of 2.5 cm mesh hardware cloth, reinforced at the edges with 1.2 cm ($^1/_2$ in.) rebar. Because of the large mesh size, the carcasses were in close contact with the ground at all times. At each examination time, the cage was removed, a tripod was set up with a hanging scale, and the carcass was suspended from the scale to determine weight loss over time. Insect fauna was visually assessed and recorded but no samples were taken and, aside from being weighed, the control carcasses themselves were not disturbed. Soil samples were taken from beneath each Group 2 carcass for later lab analysis approximately every 15 days until 167 days after death, and then again at 271 days after death. In all cases, the soil samples were processed in separate Berlese/Tulgren funnels for 24 h, to determine the change, if any, in soil fauna over time.

Group 3 consisted of two carcasses. Each carcass was placed directly on the ground. In one case, a temperature probe was inserted into the center of the carcass *via* the thoracic entrance wound to measure carcass temperature. The probe was attached to an ACR SmartReader 1 datalogger (Young Environmental Systems, Richmond, B.C.) programmed to record both ambient and probe temperature every 30 minutes. The datalogger was attached to an upright post approximately 1 m from the carcass and 60 cm above the ground. It was enclosed in a waterproof casing and covered with plywood to prevent exposure to direct sunlight. The probe was placed in position immediately after death, and was not disturbed further. At each examination time, the carcasses were visually assessed but insects were not sampled. These carcasses acted as controls, in order to determine whether the act of sampling or raising the carcasses affected the rate of insect colonization or decomposition. A rain gage was also placed at the site to determine rainfall levels.

A photographic record of all carcasses was maintained.

Results

Decomposition is a continuous process, but for convenience in discussing the results, it can be divided into stages. However, these stages do not necessarily represent the appearance or disappearance of specific species or insect groups, as these are not abrupt changes in the insect fauna (21), but rather, are recognizable stages in the physical decomposition of the carcasses. In this study, five decomposition stages could clearly be recognized, slightly modified from the six stages discussed by Payne (16). The insects collected from the carcasses over time are shown in Table 1. All the carcasses went through the stages of decomposition at the same rate, and each insect species colonized all the remains at the same time.

1. Fresh Stage (0–1 Days After Death)

This stage began at the moment of death and continued until bloat was evident. Chemical breakdown of the body occurs during this stage but few of these changes can be determined morphologically (22). No odor was associated with the remains. The internal temperature of the body dropped during this stage (Fig. 1), as the body cooled (algor mortis) (23,24). Calliphoridae, or blow flies, were attracted to the carcasses within minutes of death, and eggs were laid within 1 h of death. Most eggs were laid at the wound sites, and close to natural offices, although some were laid where the carcass touched the ground, possibly attracted to areas of body fluid accumulation and seepage. Although adult *Phormia regina* (Meigen) were seen near the carcasses, only immature *Lucilia illustris* (Meigen) were collected during the fresh stage. Adult Sarcophagidae and Muscidae also were attracted to the remains, but no immatures were collected. Adult ants also were collected from the bodies.

2. Bloated Stage (2–10 Days After Death)

This stage began when gases started to accumulate in the carcasses resulting in a definite bloated appearance. Gases from the activity of anaerobic bacteria resulted first in a slight inflation of the abdomen, followed by a gradual bloat of the entire carcass (5). The body color changed and exhibited a marbled appearance, the anus was extruded and a strong odor of putrefaction was evident. This stage ends when the body deflates, due to insects piercing the carcass (16). The bloated stage lasted up to 10 days after death in all the carcasses. Adult flies, in several families, were attracted to the remains and larval blow flies were observed. However, 2–4 days after death, heavy rainfall resulted in many eggs and larvae being drowned (Fig. 1). Fresh eggs were laid and development proceeded uneventfully. Internal carcass temperature increased considerably as maggot masses developed. The carcasses began to lose body material during the bloat stage, primarily due to maggot activity (Fig. 2). Weight loss was very rapid during this period and approximately 25% of the carcass weight had been lost by the end of this stage.

Adult Piophilidae and Fanniidae were collected but no larvae (Table 1). Adult Carnidae (*Meoneura* sp.) were first collected on day 8 and large numbers were frequently found flying above the remains. Adult Staphylinidae were observed preying on blow fly larvae, and were collected, and adult Cleridae, Carabidae and Silphidae also were collected. Reproductive ants (Formicidae) were collected by day 8.

3. Active Decay Stage (11–16 Days After Death)

The onset of this stage was marked by the complete deflation of the carcass, due to the feeding Calliphoridae larvae breaking the skin. Flesh and skin were still present. The carcasses were very wet, due to decomposition, and a strong smell was associated with the carcasses. Maximum internal carcass temperature peaked during this stage, but minimum internal carcass temperature remained low (Fig. 1). Internal and ambient temperatures fluctuated

TABLE 1—*Insects collected from pig carcasses over time in the Lower Mainland region of British Columbia.*

Decomposition stage (and days since death)	Order	Family	Genus and species	Insect stage
Fresh (0–1 d)	Diptera	Calliphoridae	*Lucilia illustris* (Meigen)	ad, imm
			Phormia regina (Meigen)	ad
		Muscidae	Not collected, so not identified beyond family	ad
		Sarcophagidae	Not collected, so not identified beyond family	ad
	Hymenoptera	Formicidae	*Lasius sp.*	ad
Bloat (2–10 d)	Diptera	Calliphoridae	*Lucilia illustris* (Meigen)	ad, imm
			Phormia regina (Meigen)	ad, imm
		Muscidae	*Musca autumnalis* De Geer	ad
			Ophyra sp.	ad
		Fanniidae	*Fannia atra* (Stein)	ad
		Heleomyzidae	*Neoleria lutea* (L.)	ad
		Dolichopodidae	*Dolichus* sp.	ad
		Carnidae	*Meoneura* sp.	ad
		Piophilidae	Not collected, so not identified beyond family	ad
		Sarcophagidae	Not collected, so not identified beyond family	ad
		Sepsidae	Not identified beyond family	ad
	Coleoptera	Carabidae	*Carabus granulatus* (L.)	ad
			Anisodactylus binotatus F.	ad
		Staphylinidae	*Creophilus maxillosus* (L.)	ad
			Tachinus crotchii Horn	ad
		Silphidae	*Thanatophilus lapponicus* (Herbst)	ad
		Cleridae	*Necrobia rufipes* (De Geer)	ad
	Hymenoptera	Formicidae	Formicinae (subfamily)	ad, repro
Active (11–16 d)	Diptera	Calliphoridae	*Phormia regina* (Meigen)	ad, imm
			Lucilia illustris (Meigen)	ad, imm
		Muscidae	*Ophyra* sp.	ad
		Carnidae	*Meoneura* sp.	ad
		Piophilidae	*Stearibia nigriceps* (Meigen)	ad
	Coleoptera	Cleridae	*Necrobia* spp.	ad
		Silphidae	Not collected, not identified beyond family	ad
	Hymenoptera	Formicidae	Formicinae (subfamily)	ad, repro
	Lepidoptera	Nymphalidae	*Cynthia cardui* (L.)	ad
Advanced (17–42 d)	Diptera	Calliphoridae	*Phormia regina* (Meigen)	ad, imm
			Lucilia illustris (Meigen)	ad, imm
		Muscidae	*Ophyra* sp.	ad
		Carnidae	*Meoneura* sp.	ad
		Piophilidae	*Stearibia nigriceps* (Meigen)	ad
			Not identified beyond family	imm
		Tachinidae	*Eutheria setifaces* Brooks	ad
		Milichiidae	Not identified beyond family	ad
	Coleoptera	Staphylinidae	*Philonthus politus* (L.)	ad
			Ontholestes cingulatus (Grav.)	ad
		Dermestidae	*Dermestes frischii* (Kugelann)	ad
			Dermestes sp.	imm
		Nitidulidae	*Omosita colon* (L.)	ad
		Silphidae	Not collected, not identified beyond family	ad
		Carabidae	Not collected, not identified beyond family	ad
		Cleridae	*Necrobia rufipes* (De Geer)	ad
			Necrobia ruficollis (F.)	ad
		Carabidae	Not collected, not identified beyond family	
	Hymenoptera	Formicidae	Formicinae (subfamily)	ad, repro
		Myrmaridae	*Alaptus* sp.	ad
	Lepidoptera	Nymphalidae	*Cynthia cardui* (L.)	ad
Dry/remains (43–271 d)	Diptera	Calliphoridae	*Phormia regina* (Meigen)	ad
			Lucilia illustris (Meigen)	ad
		Piophilidae	*Stearibia nigriceps* (Meigen)	ad
			Not identified beyond family	imm, t
		Carnidae	*Meoneura* sp.	ad
		Sarcophagidae	*Belleria melanura* (Meigen)	ad
		Sphaeroceridae	*Coprioca* sp.	ad
			Leptocera sp.	ad
		Fanniidae	*Fannia manicata* (Meigen)	ad
			Fannia canniculatis (F.)	ad
		Muscidae	*Hydrotaea dentipes* (F.)	ad
			Ophyra sp.	imm
		Drosophilidae	*Drosophila* sp.	ad
		Sepsidae	Not identified beyond family	imm
		Stratiomyidae	Not identified beyond family	imm
		Scatopsidae	Not identified beyond family	imm
		Cecidomyiidae	Not identified beyond family	ad

TABLE 1—*Continued.*

Decomposition stage (and days since death)	Order	Family	Genus and species	Insect stage
Dry/remains (43–271 d)	Coleoptera	Cleridae	*Necrobia ruficollis* (F.)	ad
			Necrobia violacea (L.)	ad
	Coleoptera	Cleridae	*Necrobia rufipes* (De Geer)	ad
			Necrobia s pp.	imm
		Dermestidae	*Dermestes frischii* Kugelann	ad
			Dermestes sp.	imm
		Staphylinidae	*Philonthus politus* (L.)	ad
			Philonthus varians (Paykull)	ad
			Aleochara curtala (Goeze)	ad
			Ontholestes cingulatus Grav.	ad
			Staphylininae (subfamily)	imm
	Coleoptera	Nitidulidae	*Carpophilus* sp.	imm
			Omosita colon (L.)	ad
		Hydrophiloidae	*Sphaeridium bipustulatum* (F.)	ad
			Cercyon haemorrhoidalis (F.)	ad
		Carabidae	*Carabus granulatus* (L.)	ad
			Pterostichus melanurus Illiger	ad
			Calathus fuscipes Goeze	ad
		Silphidae	*Nicrophorus defodiens* (Mannerheim)	ad
		Histeridae	*Carcinops pumilio* (Erichson)	ad
		Argyrtidae	*Necrophilus hyrophiloides* Guérin-Méneville	ad
			Necrophilus sp.	imm
	Hymenoptera	Formicidae	Formicinae (subfamily)	ad, repro
			Formica sp.	ad
	Psocoptera	Liposcelidae	*Liposcelis* sp.	ad

NOTE:—ad = adults, imm = immatures, t = teneral, repro = reproductive adult Hymenoptera.

considerably, with a greater difference seen between internal maximum and minimum temperatures than between ambient maximum and minimum temperatures, however, both maximum and minimum internal carcass temperatures followed the same trends as ambient temperatures.

The carcasses were reduced to less than 50% of their original weight by the end of the active decay stage (Fig. 2). Maggot masses were found throughout the body. Coleoptera and adult Diptera other than Calliphoridae were collected (Table 1) but the dominant insects by far were larval Calliphoridae.

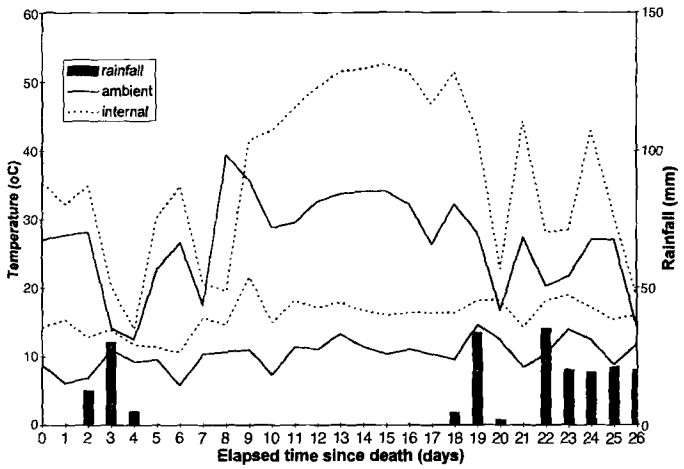


FIG. 1—*Maximum and minimum internal carcass temperatures of a pig carcass measured with an internal probe every 30 minutes, maximum and minimum ambient temperatures, measured every 30 minutes, and daily rainfall, during the first 26 days of decomposition.*

4. Advanced Decay Stage (17–42 Days After Death)

At this stage, much of the flesh had been removed. Maggots left the remains as prepupal insects during this stage and internal carcass temperature dropped rapidly (Fig. 1). Twenty-six days after death the internal temperature probe was exposed due to insect removal of surrounding flesh and skin, so the probe was removed from the carcass. Less odor was associated with the remains. Weight loss continued throughout this stage but at a slower rate than in previous stages. During periods of heavy rain, weight appeared to increase, due to the remaining skin and flesh absorbing water.

Piophilidae larvae (mostly third instar) were collected first 29 days after death, and were collected regularly throughout this stage. Dermestidae larvae were collected first 21 days after death, though

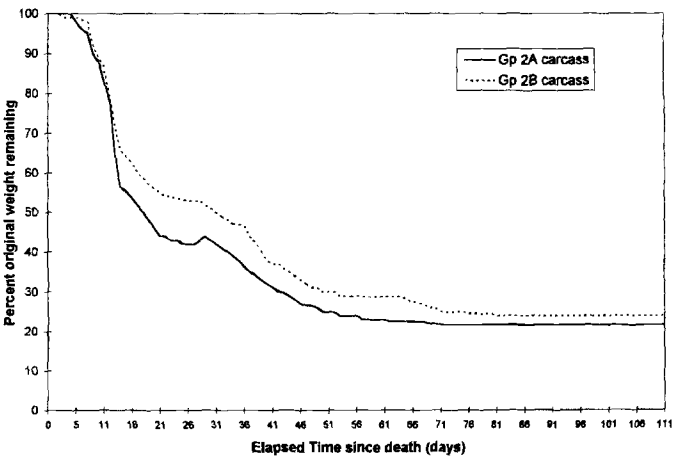


FIG. 2—*Percentage weight loss over time in two pig carcasses during decomposition.*

not commonly. Adult Dermestidae were commonly found from 24 days postmortem. The larvae were only identified to genus, but as only one adult species was collected throughout this study, *Dermestes frischii* Kugelman, the larvae probably belonged to this species also. Staphylinidae, Nitidulidae, Silphidae, Cleridae and Carabidae also were collected (Table 1). Carnidae continued to be found in abundance on and around the carcasses, and appeared to be feeding on body fluids on the vegetation.

5. Dry/Remains Stage (43 Days+ After Death)

In this stage, very little of the carcasses remained except bones, cartilage and some skin. There was little or no odor associated with the remains by this time. Approximately 20% of the carcasses remained, by weight (Fig. 2) during this stage. The carcasses entered this stage by late July and continued in this stage through the fall and winter, with some small amounts of skin still present into early spring. The experiment was terminated in late spring.

More species of Diptera and Coleoptera were associated with this stage than any other (Table 1). The first adult Piophilidae to emerge from the remains were seen on day 73 (collected as teneral insects), but larval Piophilidae continued to be found on the remains until more than 167 days after death. Adult Carnidae were still collected during the early part of this stage, but not in the numbers seen earlier. Also, adult Calliphoridae were attracted to the remains but did not lay eggs. Adult and immature Muscidae were collected, together with adult Sarcophagidae, Cecidomyiidae and Sphaeroceridae, and larval Sepsidae, Stratiomyidae, and Scatopsidae. Dermestidae larvae were commonly collected until 111 days after death, but neither larvae nor adults were collected after this time. Larval Cleridae were first collected 94 days after death, and adults continued to be found until more than 167 days after death. Adult Staphylinidae continued to be collected throughout this stage, and larvae were found by day 74. The first larval *Carpophilus* sp. (Nitidulidae) were collected 64 days after death and continued to be collected until more than 128 days after death. Adult *Necrophilus hydrophiloides* Guérin-Méneville (Argyrtidae) were first collected 128 days after death, and larvae of this genus were collected 167 days after death.

By 271 days after death very little of the remains were still present, and the only insects associated were incidental.

Soil Fauna

Arthropod fauna in the soil beneath the carcasses changed dramatically over time with a rapid drop in biodiversity within the first 15 days after death (Table 2). Species numbers dropped to two 15 days postmortem, and a different faunal assemblage was collected after 29 days and more had elapsed. This coincided with the active and advanced decay stages, during which times much of the decomposing body fluid seeped into the ground under and surrounding the remains. The vegetation under and surrounding the remains for approximately 20–30 cm was killed by the body fluids. The majority of specimens collected were in the Class Acari, although some smaller Coleoptera were collected more easily in soil samples than by hand collection, such as *Carpophilus* sp., which were collected regularly from the soil from day 64 to day 167 and were found to be extremely abundant by day 128 (>200 in a soil sample), whereas they were no longer collected from the carcasses themselves after day 128. Also, *Carcinops pumilio* (Histeridae) was collected from the soil from day 94 to day 167, but was not collected by direct hand collection. The soil fauna and the vegetation had not returned to normal by 271 days postmortem.

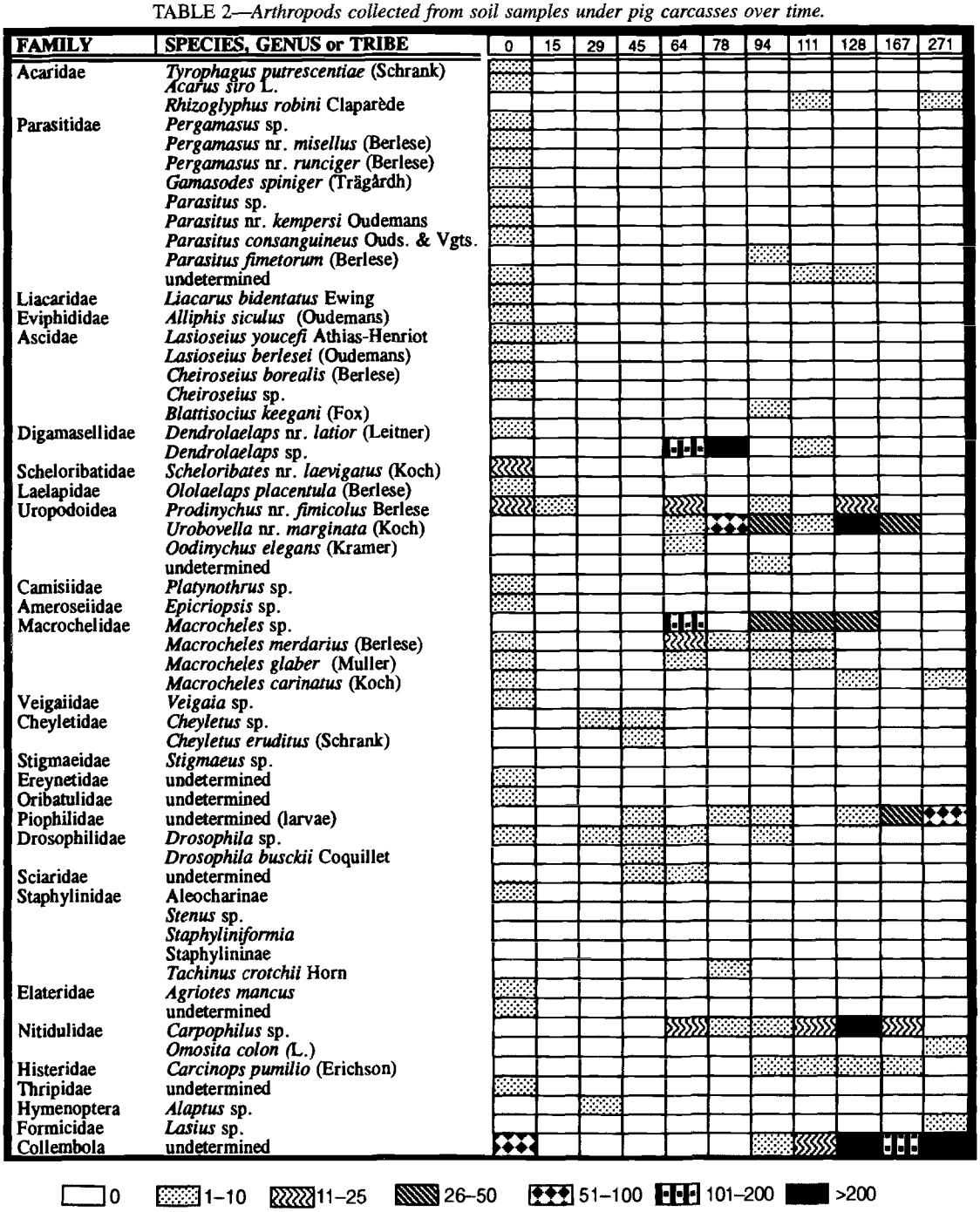
Discussion

Pig carcasses were colonized by a succession of insect species in the Lower Mainland of British Columbia in open ground, from immediately after death until more than nine months after death. This is a long colonization time compared with that reported from many areas. Early and Goff and Tullis and Goff, using small carcasses in tropical regions found that decomposition was complete, with few further insects attracted after three months (6,7). Even in more temperate regions in the continental U.S.A., pig carcasses entered the remains stage within four weeks of death (16). Carcasses in the present study spent two days in the fresh state, which is similar to that reported elsewhere (6,7,16), but longer in all other stages. This is most likely a reflection of the very different meteorological conditions in southwestern British Columbia. It may be related to carcass size as, although both Payne (16) and Tullis and Goff (7) used pig carcasses, both were considerably smaller than 22 kg. However, this is unlikely as adult human corpses completed the decay process in 61 and 26 days in spring and summer respectively in Tennessee (10).

The carcasses remained in the bloated stage for longer than has previously been reported for carcasses exposed to insects in summer (6,16). However, the end of bloat is usually signified by the penetration of insect larvae into the body, resulting in the release of gases (16). Carcasses protected from insects remain in the bloat stage for much longer than those open to insect colonization (12, 16), and generally decay at a reduced rate (25). In this study, although insects colonized the remains immediately, heavy rains 2–4 days after death resulted in many of the eggs and early instars drowning. Fresh eggs were laid, but larval development on the body was delayed several days, probably resulting in the delayed termination of bloat. Considerable precipitation is common in southwestern British Columbia, so this may occur in many cases in this area.

Decomposition studies worldwide have used a variety of different carcass types and sizes including cats (6), dogs (17,26), guinea pigs (18), mice (27), foxes (28,29); lizards and toads (30); turtles (12), rabbits (15), elephants (14), impala (13) and humans (10). Carcass type and size can have an effect on decomposition rate and insect succession. Denno and Cothran (31) found that carcass size had a direct relation to fly populations, and work by Hewadikaram and Goff (32) supported this, but also indicated that there were no size-related differences between 8.4 kg and 15.1 kg pig carcasses with respect to composition of the insect fauna or patterns of succession. It might be expected that small carcasses would decompose more rapidly than larger carcasses, but because the larger carcass attracted more flies, it supported a larger number of maggots, so decomposition, was actually faster in the larger carcass, due to maggot removal of body material (32). However, extremely small carcasses such as those of lizards and toads (30) and shrews, mice and other small rodents (16) have been reported to decompose very quickly, with no marked stages of decomposition. Coat type may also have an effect on the insects attracted to the body. Human bodies are obviously the ideal research material, but it is not usually possible to obtain large numbers of human bodies at one time, so studies using such carcasses have invariably had only one replicate (10,33). Therefore, 22 kg pigs have been recommended as suitable human models for decomposition (34). They are omnivorous, so have similar gut fauna, are relatively hairless and have skin that is very similar to that of humans. Twenty-two kilograms is approximately equivalent to that of an adult human male torso, where decomposition is centered. Studies here have been related to actual human cases of known time of death, and

TABLE 2—*Arthropods collected from soil samples under pig carcasses over time.*



the pig model appears to relate well to human cases. In this area, insects are commonly found on human remains months after death (35) and can be found several years after death although insects have usually been found to be a reliable indicator for only the first 18 months after death in southwestern B.C. However, insects can be used to indicate season of death for a number of years.

All seven carcasses decomposed at the same rate, entering each stage synchronously, and were colonized by the same insect species at the same time, or within a day of each other, indicating that the acts of sampling group 1 carcasses and weighing group 2 carcasses did not have an effect on decomposition or insect succession. Also, this confirms that placing the carcasses (group 2) on mesh platforms for the purpose of weight measurements, did not affect insect colonization. Many previous studies have involved placing the carcass on some sort of mesh platform, or cage base (6,7,10,16, 32,36), but most did not compare carcasses on mesh *versus* those directly placed on the ground. This study indicated that a thin, large spaced mesh does not impede insect colonization, nor affect rate of decomposition.

The weight of the carcasses did not change for the first five days, but then dropped rapidly during the bloated and active decay stages, and the remains had been reduced to less than 50% of their original weight by the advanced decay stage. The majority of the body material was removed by maggot activity between 7 and 30 days postmortem. Maggots have been shown to remove the majority of the carcass in both tropical (6) and temperate regions (12,

31), and decomposition is slowed down when insects are prevented from accessing the body (16). By 51 days after death, only bones, cartilage and some skin remained, representing approximately 25% of the original carcass weight. Insects were still present on the remains and were feeding, but had little impact on overall carcass weight.

Internal carcass temperature was greater than ambient temperature, and this was particularly apparent from 9 to 18 days postmortem. However, although ambient temperatures obviously fluctuate over a wide range in a 24 h period, it is usually assumed that internal carcass temperature fluctuates less, remaining at a higher, more constant temperature than ambient (37). However, in most decomposition studies, only a single internal temperature is given, with no maximum and minimum range indicated (6,16,36). Our work has shown, however, that, although internal carcass temperature does increase considerably during active decay, there is greater fluctuation in internal than ambient temperature, with diel differences of more than 35°C. Temperature has a considerable effect on insect development. Because the internal carcass temperature fluctuates so greatly during a single day, it is important to recognize that a single reading at a death scene during an investigation may give an erroneously high reading for overall analysis. Also, despite the fact that the internal carcass temperature frequently reached extremely high temperatures during the day, it must be realized that an individual maggot is very unlikely to be living at such high temperatures for any length of time. Maggots in a mass are constantly moving, down to the feeding site, then back out to the exterior of the mass (personal observations). Therefore, despite high internal mass temperatures, the actual temperature at which an individual maggot develops is unknown. It is probable that it is somewhere between internal and ambient temperatures, but as both fluctuate considerably over a 24 h period, it is very important that this factor is investigated further as temperature is the key to estimating time of death based on maggot development. As well, the internal temperature of the carcass can only have an effect on some of the immature stages of blow fly development as the prepupa and pupa develop away from the carcass.

The first insect species attracted to the remains to lay eggs was *Lucilia illustris*. Adults were attracted within minutes and eggs were laid within less than 1 h of death. In many previous studies, previously frozen or refrigerated carcasses have been used (7,9, 10,16). Freezing can have an effect on bacterial decomposition (38), but has not been reported to have an effect on insect succession patterns (16). Also, although little decomposition can have taken place, it is still possible that, as death took place some time before placement, early decompositional changes could make such remains attractive to insects more rapidly. We wanted to ensure that data on colonization times were from time since death, rather than time since placement. This study confirmed that insects are attracted to the remains within minutes of death. Later studies have confirmed that Calliphoridae will oviposit within minutes in this area (unpublished data). Calliphoridae are attracted to carrion at different stages of early decomposition. Some early reports of carrion succession have stated that *Lucilia* sp. is a later colonizer, arriving only when odor can be detected (20,39), but *Lucilia illustris* was the first to be attracted to fresh remains in this study, when no odor was present, and has been found to be an early colonizer in other areas (28,40–42). In some cases, *Lucilia* sp. have even been found to anticipate death (43). *Phormia regina* adults also were attracted soon after death, but no eggs were laid until day 2. It has previously been reported that *Phormia regina* is not a pioneer species on carrion, and usually arrives later than other Calliphoridae, preferring to colonize remains several days after death (9,42), irrespective of carcass size (15). A study in Missouri in which several hens were killed at the same time, but exposed to insects at different times, showed that a few *Phormia regina* were collected as adults in the first 24 h, but significantly more were collected on carrion 24–48 h old, and significantly more again between 48 and 72 h. A few eggs were collected during the first 24 h, but the majority were collected more than 24 h after death (44). No *Calliphora* spp. were collected in our study, which may be due to the preference in this group for shady conditions (5) as these carcasses were placed in direct sunlight. However, *Calliphora vicina* Robineau-Desvoidy has been collected in both sun and shade in other areas (27).

Dermestidae larvae were first collected 21 days after death, in the early stages of advanced decay, when some flesh still remained, although more were collected after 43 days postmortem. Adult Dermestidae were commonly found from 24 days postmortem. This is earlier than is usually reported for this group, particularly for immatures. A few adult specimens were collected as early as 3 to 5 days after death and 10 days after death in Hawaii (6,32), although larvae were not reported until later (6). However, in such tropical conditions, decomposition occurs much faster than in temperate climates. In most studies, this family is considered to be the last group to feed on the remains, with the majority of adults and larvae being collected in the final stages of decomposition when only skin and bones remain (5,6,10,17,41,45,46), although the actual postmortem interval varied with geographic region. The time of colonization of carrion will vary with geographical location, and there is no previous information from British Columbia. The only other study of insect succession on carrion in Canada states that Dermestidae, including *Dermestes frischii*, were not collected on human remains until 3–6 months after death, despite compelling evidence of a case in which *Dermestes* sp. were found less than 5 weeks after death (20). The authors stated that even in extremely dry experimental conditions, Dermestidae beetles could not be induced to colonize the remains of human infants in less than two months (20). However, this report is of some age, and comes from the Province of Quebec, which has different biogeoclimatic conditions than those of B.C., therefore further research is required in other provinces to determine colonization and decomposition rates in a variety of areas.

Staphylinidae adults and larvae thrive in many types of waste matter, are frequently predaceous on Diptera larvae, and many are active all year (17). Adults were found on the body very shortly after death, but larvae were not collected until 78 days after death, confirming previous observations (7,10,17,41,46).

Adult Silphidae were collected throughout decomposition in this and other studies (10,17), although they have been reported only from the later stages of decay in some areas (39,46).

In previous studies, a number of Histeridae have been collected throughout decomposition (10,17,46), however, only *Carcinops pumilio* (Erichson) was collected in our study.

Adult Cleridae were collected early in decomposition, but larvae were not collected until the dry/remains stage, 94 days after death. Previous reports confirm these observations (10,17,46), although larvae were rarely collected in most previous studies. Most species in this family are predaceous as both adults and larvae, but can also be found on a variety of decomposing matter (46). *Necrobia* spp., which were collected in this study, are thought to differ from the general clerid feeding habits, and to subsist primarily as scavengers (47).

Adult Nitidulidae (*Omosita colon* (L.)) were first collected 22 days after death and continued to be collected throughout the advanced and dry/remains stage. Larval *Carpophilus* sp. were only found in the dry/remains stage and were found in increasingly large numbers from 64 days after death, peaking at 128 days after death. This supports other studies in which the majority of the Nitidulidae were found in the later stages of decomposition (10,17,46).

Piophilidae larvae also were collected earlier than has previously been reported, 29 days after death. In Quebec (20), and in France (39) they were reported to be attracted to remains 3–6 months after death, arriving after Dermestidae. In Illinois, adult Piophilidae were first attracted to the carrion during bloat, but the majority arrived during the decay stage, although no larval specimens were collected (48). However, Piophilidae larvae were collected from a single dead fox in England 30 days after death (28), from carcasses in Hawaii 33 to 36 days after death (49) and have been collected from human remains 26 days after death in British Columbia (35). This study confirms these earlier observations that Piophilidae arrive earlier in the successional sequence in some areas and habitats than previously thought.

In some cases, time of carrion colonization may be more closely related to peak seasonal appearance of species, rather than decompositional state of the remains. *Necrophilus hydrophiloides* was first collected 128 days after death, in mid-October, which could indicate that it is a later succession insect, attracted only to the latter part of the dry/remains stage of decomposition. However, peak adult activity is reported between November and May (50), indicating that it was collected from remains early in its season. Further carrion studies in more than one season are required to determine the successional sequence of such insects.

Ants (Hymenoptera; Formicidae) were collected from the remains throughout the decomposition period, feeding on both carrion and insects. Fuller (41) suggested that ants were not regular carrion inhabitants as they were only found on carcasses near nests, but this study found them on all carcasses and at all stages of decomposition, supporting Payne's (51,52) contention that ants are common carrion insects. In some areas, the removal of dipteran eggs by ants, particularly fire ants (*Solenopsis* sp.), can have a major effect on decomposition rates (6,53–56), and some workers have found that other species of ant also can have a significant effect on decreasing the decay rates in other geographic areas (30, 42). The ant species found in this study, although present throughout decomposition, did not appear to have a major impact on decomposition rates, but the effects of ants on carrion reduction is presumably dependent on species, abundance and geographic region.

Only one Lepidopteran, *Cynthia cardui* (L.) (Nymphalidae), was collected from the remains during the active and advanced decay stages, and appeared to be feeding on the carrion. This species has been reported to feed only on plants (57), but Payne (58) reported a variety of Lepidoptera, including some in the family Nymphalidae, which were attracted to carrion to feed, and Milne and Milne reported that woodland members of the family Nymphalidae feed on the juices of rotting fruit, organic wastes or on the fermenting sap of trees (59).

After 271 days postmortem, no further insects were collected from the remains themselves. However, the effects of decomposition were still evident in the soil fauna. A large number of species were found prior to carcass deposition, but many of these were not collected under the remains again for 64–94 days postmortem, and some were still not found at the termination of the experiments, indicating that the soil had not yet returned to pre-carcass condition. In Western Australia, studies showed that soil fauna and plant growth had not returned to pre-carcass conditions one year after death, although soil fauna were normal within 20 cm of a small carcass (18). Several mite species which were not present, or present in low numbers, before carcass deposition were found to increase in abundance over time, notably *Dendrolaelaps* sp. (Digamasellidae), *Urobovella* nr. *marginata* (Koch) (Uropodoidea) and members of the Machrochelidae. Members of these groups are known to feed on soil fauna and arthropod eggs (60). Also, there was a dramatic reduction in the number of species found beneath the carcasses, with species/taxa numbers dropping from over 30 prior to carcass placement to two 15 days later. Further work is required in this area, but it appears that the composition of the soil fauna and the community biodiversity may be used to estimate time of death for a longer period of time than carcass fauna alone. Studies in tropical areas have indicated that soil arthropod succession may be very valuable in estimating time of death (61).

Insect succession on carrion, when known for a given area, can be very useful in estimating time of death. This study provides valuable information on carrion fauna and their times of colonization of a corpse in summer, in direct sunlight, in southwestern British Columbia in the Coastal Western Hemlock biogeoclimatic zone. However, further work is required in a variety of habitats, such as shade, below ground, and in different seasons, and geographic areas of the province to provide a complete database. This work is presently underway.

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