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Insect succession and decomposition patterns on shaded and sunlit carrion in Saskatchewan in three different seasons

Barbara J. Sharanowski [a,*], Ernest G. Walker [b], Gail S. Anderson [c]

[a] University of Kentucky, Department of Entomology, S-225 Agricultural Science Center North, Lexington, KY 40546-0091, USA
[b] Department of Archaeology, Anthropology & Archaeology Building, 55 Campus Drive, University of Saskatchewan, Saskatoon, Saskatchewan S7N 5B1, Canada
[c] School of Criminology, Simon Fraser University, 8888 University Drive, Burnaby, British Colombia V5A 1S6, Canada

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Abstract

A study was conducted on decomposition and insect succession in the Prairie Ecozone of Saskatchewan in the year 2000. Eighteen domestic pig carcasses (42–79 kg) were employed as human models for applications to future homicide investigations in this region. Two major variables were considered including the effect of season and habitat (sun versus shade). Research was conducted over 25 weeks, spanning three seasons: spring, summer and fall. Ambient temperature, internal carcass temperature, faunistic succession over time, and the rate of decay were all compared for each experimental variable. Results indicated that habitat was only a factor in the decompositional rate of carrion in the spring season. The ambient temperature was the chief factor determining the seasonal variations in decay rate. Maximum internal carcass temperatures always coincided with the presence of 3rd instar larvae. Patterns of insect succession occurred in a predictable sequence that varied across different habitats and seasons and was unique compared to previously published studies. Carcasses placed in spring and fall attracted a more diverse assemblage of insects than summer-placed carrion. Sun-exposed carrion also had greater variation in fauna than shaded carrion in spring and fall. Members of Silphidae were the first coleopteran colonizers in all habitats and seasons. This paper also marks the first record for Cochliomyia macellaria (Fabricius) in Saskatchewan.

Keywords: Forensic entomology; Insect succession; Carrion; Postmortem interval; Decomposition

1. Introduction

Insect colonization of carrion has been demonstrated to occur in a predictable sequence [1–7]. The specific period of colonization of certain insects on carrion can be established as forensically significant insects are either attracted to specific products of decomposition or are predators on these necrophagous insects [8–10]. If the sequence of insect succession on carrion is known for a given geographical region and a specific set of variables, it can be compared against collected species from bodies of unknown time of death to yield the postmortem interval, provided circumstances are similar [10]. However, intervals based on succession patterns require knowledge of insect fauna in the geographic region in which the corpse is discovered, as species vary widely with geographic region [5]. Ambient temperature, season, and microclimate of the postmortem habitat also play major roles in the determination of the invertebrate assemblage on carrion [8,9].

For example, Shean et al. [11] examined the effect of sunlit versus shaded habitats on insect succession and concluded that carrion exposed in the sun demonstrated a faster rate of decomposition and thus, a shorter period of insect colonization. Several researchers have examined the differential effects of season on necrophagous fly activity [12,13], decomposition [14,15], and insect succession [7,16], each concluding that season has a major effect on the invertebrate assemblage discovered on carrion and the time of colonization of insects. Thus, it is crucial to examine seasonal insect activity on carrion in specific geographic regions and various habitats within these regions.

* Corresponding author. Tel.: +1 859 257 3169; fax: +1 859 323 1120.
E-mail addresses: rhubarb@uky.edu (B.J. Sharanowski), ernest.walker@usask.ca (E.G. Walker), ganderso@sfu.ca (G.S. Anderson).

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Locally generated data on arthropod succession and development increases the precision of postmortem interval estimations [4]. The present study was designed to investigate the pattern and rate of decomposition and arthropod succession on carrion in two different habitats (sun-exposed versus shaded) and in three different seasons (spring, summer, and fall). The main objective was to provide entomological data that can be employed in forensic cases in Saskatchewan and other similar biogeoclimatic regions.

2. Materials and methods

2.1. Study site

The study site was located on University of Saskatchewan research land in Saskatoon (52°08′54.39N 106°37′23.61W), in the heart of the Moist Mixed Grassland Ecoregion of the Prairie Ecozone of Canada. In its native form, this region is characterized by dark, well drained soils, broad-leaved herbs, mixed grasses, and deciduous shrubs. However, over 80% of native land has been converted for the cultivation of cereal grains. Approximately half of the University research land had also been cultivated for agricultural studies. For each season, three shaded and three fully sunlit sites were selected. Sites for carcass placement were chosen on fringe areas, within shrubs away from the crops (shaded sites), or on the edges of cultivated land (sunlit sites). Each site was approximately 50 m apart to minimize crossover of insects. Shaded sites were chosen for maximum shade throughout most of the day. Depending on the position of the sun, the carcasses were exposed to streams of sunlight through gaps in the overhanging vegetation. Sun-exposure through vegetation usually covered less than 20% of the carcass and lasted 4 h or less. The pigs located in sun-exposed sites were placed in open areas devoid of overhanging vegetation to prevent late afternoon shadows.

2.2. Experimental animals

A total of eighteen domestic swine, *Sus scrofa* Linnaeus, were obtained from the Prairie Swine Centre in Saskatoon. Weighing between 42 and 79 kg, these pigs were chosen to simulate the average size of an adult female. This range falls into the mid-weight category established in Komar and Beattie's [17] research on decay rates and carcass size, shown to be an appropriate size model for human decomposition. On the delivery day in each season, pigs were weighed, ear tagged, and then euthanized with a high-powered bolt to the frontal portion of the skull, with the time of death recorded. The bolt-technique is the standard method for the slaughter of swine at the Prairie Swine Centre and was approved by the University of Saskatchewan Committee on Animal Care and Supply. The pigs were immediately delivered postmortem to the research site in a covered 4 × 4 trailer and prepared for placement at the chosen study sites.

2.3. Field protocols

Experimental protocols were modified from that of Anderson and VanLaerhoven [5]. The experiments have been modified for cost-effectiveness, without sacrificing validity. For example, Anderson and VanLaerhoven [5] employed five pigs per variable, two of which acted as control carcasses without insect collection. However, they concluded that representative insect collection from carrion does not impede the natural succession of the insects. Additionally, a subsequent study by De Jong and Hoback [18] provided further evidence that repeated sampling does not impact the qualitative assessment of the natural community of species on carrion. Thus, three pig carcasses per habitat were employed. All efforts were made to keep carcass disturbance to a minimum during sampling. Qualitative sampling data from each carcass was pooled for each experimental variable. If the arrival or departure time of a specific insect was not the same across all three pigs in a given variable, the species was reported as unpredictable (see Section 3).

Individual pigs were measured for girth and dressed with one piece of clothing. Next, the pigs were wounded with a non-serrated knife in the thoracic region. One pig in each of the two habitats had a data logger (TBI32-0.5 + 37) Hobo®, Hoskins Scientific, Vancouver, British Columbia) inserted by hand approximately 5 cm into the thoracic wound to record internal carcass temperature every 30 min throughout the experiment. The data loggers were small and round (~4 cm diameter) with a recording range from −5 °C to 37 °C (±0.1 °C accuracy/resolution). There were several occasions when the temperature was outside of the accurate range of these data loggers, which is marked as a plateau at the lower and upper range limits for all temperature graphs. The pig carcasses were placed atop wire mesh (2.5 cm grid) approximately 0.5 m longer than the length of the pigs. All pigs were placed on their side. Cages, made from PVC piping and wire mesh, were placed atop the pigs and secured with wire. The cages and underlying wire mesh served to minimize potential scavenging by vertebrates. Another data logger was attached to the cage of the same two pigs that had the internal data loggers. This logger recorded ambient temperature every 30 min throughout the experiment. One pitfall trap was placed at each site to collect insects throughout the day. After carcass placement, a sketch of the area was completed noting site location, direction of the carcass, position of the data loggers and pitfall traps. All pigs were placed within 3 h of the time of death.

In the first week after placement, observations, photographs, temperature readings and collections were made daily at varying times of the day (between 7:00 am and 7:00 pm). For the remainder of the experiment, collections were made every 2–3 days. Observations were made of the decompositional state and of the insects collected and seen. Temperature readings were completed with a hand thermometer for carcass skin temperature and core maggot mass temperature when large aggregations were witnessed. The fieldwork in its totality occurred over 25 weeks, from May 17 to October 26, 2000, spanning the three seasons in which insects are most active in Saskatchewan. The spring experiment was completed from May 17 to July 18, the summer experiment lasted from July 19 to August 31, and the fall experiment was performed from September 1 to October 26.

During collection days, representative samples of immature and adult insects were collected on and in the carcass, as well as the surrounding soil. While all insects observed were sampled, there was a definite focus on flies and beetles. Adult flies were collected with an aerial sweep net and then transferred to 70% alcohol. Flies were labeled as teneral adults if the cuticle was relatively pale and soft compared to the mature adult. Adult beetles, immature insects and other hard-bodied crawling insects were collected by hand or with forceps and immersed in 70% alcohol.

Soil samples were taken on occasion, especially after the observation of pupae. Soil was sifted through a mesh strainer to collect any burrowing insects or immature flies that had pupated in the soil. While beetles were preserved, dipteran pupae were placed in jars with wet tissue paper and sugar and covered with paper towel secured with rubber bands. These jars were then transferred to a growth chamber within 3 h of collection to be reared to adulthood.

For each carcass, approximately 20 immature fly specimens were collected from every distinct maggot mass on the body. Approximately half of the specimens collected were preserved while the other half were kept alive for rearing. The live specimens were placed in jars atop a layering of beef liver and wet tissue. The jars were covered with paper towel, secured with rubber bands and transferred to a growth chamber. All samples were labeled with the date and time of collection, the carcass number, the area of the carcass the samples came from, and the stage of development at the time of collection.

Insects collected for rearing were taken to the Department of Agriculture phytotron facility at the University of Saskatchewan. The growth chamber conditions were kept constant at 22 ± 0.2 °C with a 16:8 light:dark cycle and 65% relative humidity. Insects in the chamber were checked every 2 days. Upon adult emergence, after cuticular hardening and pigmentation, the adults were immersed in 70% alcohol and relabeled.

All insects were identified to the minimum of the family level with several entomological keys [20–29]. All efforts were made to identify Dipteran and Coleopteran members to the species level.

2.4. Analyses

The Student's *t*-test was employed to compare the mean daily temperatures between the sun-exposed and shaded sites for each season separately. For the *t*-test, the mean temperatures were derived from the average of every temperature

reading (every 30 min) in each habitat for a 24-h period from 12 am to 11:59 pm each day. For test validity, all treatments were tested for equal variance at a 99% confidence interval.

3. Results

Results have been divided into each seasonal experiment for ease of discussion and comparison between habitats. Although decomposition and insect succession are discussed in terms of decompositional stages (*sensu* Payne [1]), it is only for convenience and for comparison with insect succession studies in other geographic regions. Although insects of several orders may inhabit a corpse, the taxa that colonize carrion in a predictable sequence are the most forensically significant. Taxa that reoccur on a carcass, with successive visitations and absences, are less reliable as indicator species for postmortem interval estimations [30]. For terrestrial locations, members of the orders Diptera and Coleoptera are typically the best indicators for postmortem interval estimations based on succession [4]. Furthermore, carrion-frequenting flies and beetles are the most active, abundant, and predictable insects as they are necrophagous, predaceous on necrophagous insects, or both [8]. The present study details patterns of decomposition and highlights the predictable succession of dipteran and coleopteran taxa for Saskatchewan. Additionally, intermittent taxa are highlighted in succession tables. Although many incidental and forensically insignificant insects were collected, they are not reported in the results.

3.1. Spring experiment

3.1.1. Temperature data

Ambient temperatures for both the sun-exposed and shaded sites are presented in Fig. 1. Temperatures at the sun-exposed site exhibited a greater fluctuation in range, typically higher during the day and lower during evening hours than the shaded site. For the duration of the spring experiment (May 17–July 18), the mean temperature at the sun-exposed site was 17.8 °C. The mean temperature for the shaded site was 15.4 °C, which was significantly different from the sun-exposed site ($p = 0.01$).

There was a striking difference in the internal carcass temperatures between the sun-exposed and shaded sites, with a significant difference between the means of the two treatments ($p = 0.01$). The average internal temperature over the duration of the experiment was 26.0 °C and 18.2 °C at the sun-exposed and shaded sites, respectively (see Fig. 1). Only one pig in each habitat had a data logger recording internal carcass temperature. Thus, the measurements do not reflect any potential individual variation that may have occurred across carrion in a given habitat.

By day 3, average internal carcass temperatures were consistently higher in the sun-exposed carcass, with internal temperatures reaching a maximum disparity between habitats on day 40. The average internal carcass temperature at the sun-exposed site was close to or above maximum ambient temperature from day 14 to day 47. Dips in internal temperature after periods of maximum recordings in sunlit carrion during this period correspond with major waves of post-feeding larval migration. In contrast, internal carcass temperatures at the shaded site did not approach maximum ambient temperature until day 21. On days 31–33 at the shaded site, internal temperatures soared above the maximum ambient temperature, reaching a peak on day 32.

3.1.2. Decomposition

The fresh stage begins with death and ends when bloating is initiated. In spring the fresh stage lasted from day 0 to day 1 for sun-exposed carcasses. The fresh stage was extended slightly in shaded carrion from 0 to 2 days postmortem. The defining characteristics for each stage of decomposition for both sun-exposed and shaded carcasses are summarized in Table 1. Additionally, temperature data and precipitation levels are summarized across each stage of decay in Table 1.

The beginning of the bloated stage was marked by the slow accumulation of gases, first exhibited as a slight bloat in the abdomen on day 1 for sun-exposed carrion and day 2 for shaded carrion. By day 2, abdominal bloating increased in sunlit carcasses and extended to the posterior regions of the body. On day 3, bloating was obvious and had spread to the limbs, anus, and head. For shaded carrion, bloat initiated on day 2 in the abdominal area, but did not spread to the remainder of the body until day 6, and did not peak until day 9. The temperature differential in both ambient and internal readings between the two habitats accounts for the slower rate of decomposition at the shaded sites (Table 1).

The end of the bloated stage is typically marked by the deflation of the carcass due to insects piercing the skin [1,5]. For carcasses in both habitats, deflation occurred over a period of several days, typically starting in the head region, then occurring in the extremities and posterior, and lastly in the abdomen. Deflation was always most noticeable where maggot activity was the greatest. These regions included those areas with natural orifices, such as the eyes, ears, nose, mouth, and anus, and the thoracic region where the artificial wound was created. Maggots were tightly packed into natural body orifices, slowing gaseous diffusion to the air.

A better marker for the end of the bloated stage and beginning of the active decay stage was evidence of liquefaction. The ground surrounding the carcass became wet as the gaseous pressure finally forced fluids out of natural orifices. The appearance of the liquid was frothy, resembling muddy dishwater. This event was associated with a burst of maggots being forced out along with the fluid. Evidence of liquefaction first occurred on day 12 for sun-exposed carcasses and day 15 for all shaded carcasses.

During the active decay stage, the carcass became entirely infested with maggots in all stages of development. Insects devoured extremities such as the head, anus, and limbs and left the remaining skin perforated. The odor of decay increased dramatically and became putrid and offensive. Clothing became soaked with putrefactive liquids and eventually became a growth medium for mold. The clothing also trapped escaping gas as deflation ensued. Outer edges of skin and the underlying

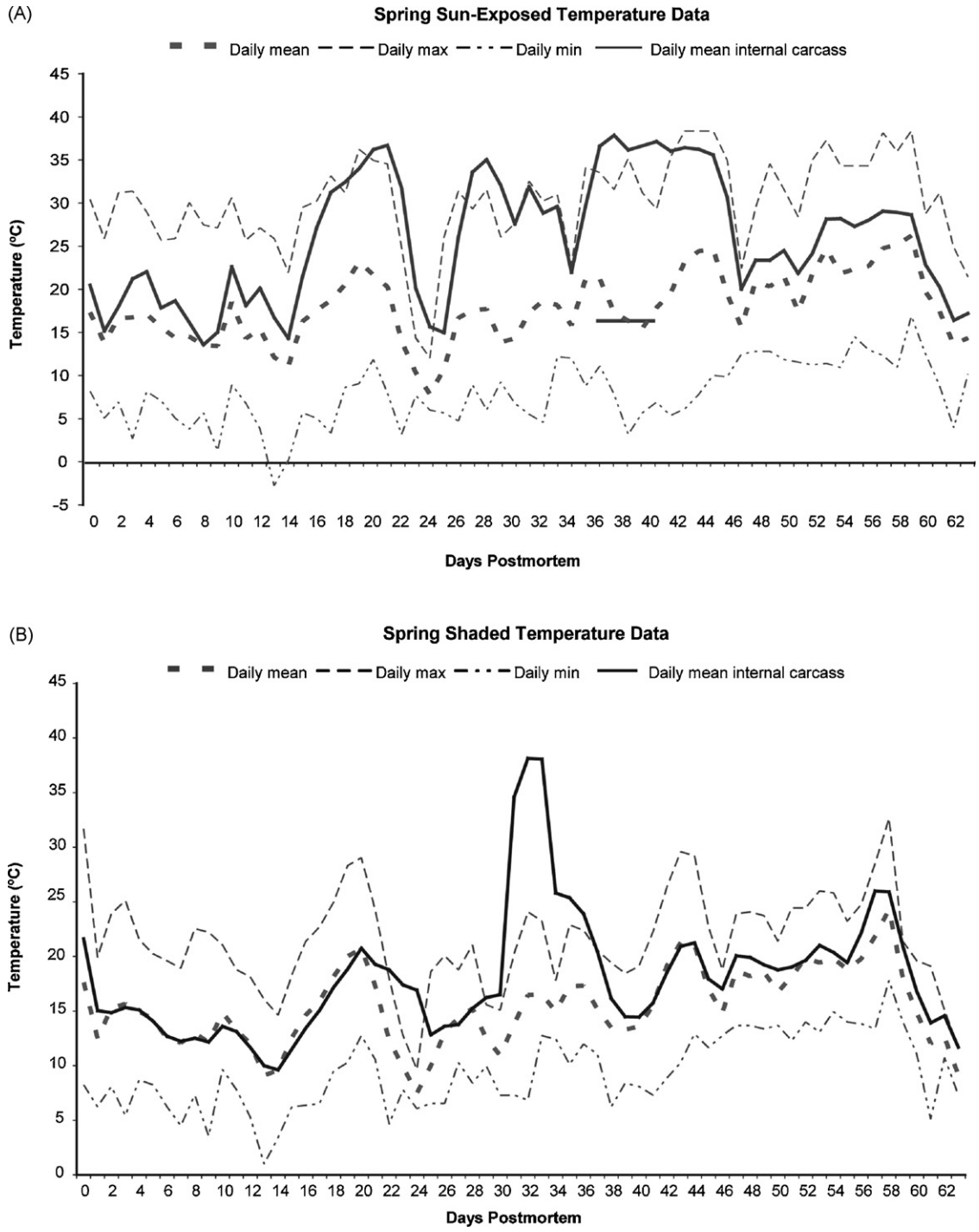

Fig. 1. Summary of temperatures recorded in the spring experiment. Accurate temperature range of data loggers was −5 °C to 37 °C (±0.1 °C accuracy/resolution). (A) Ambient and internal carcass temperature for sun-exposed site in spring from May 19 (day 0) to July 19 (day 62), 2000. Overall ambient and internal temperature means: 17.83 °C and 25.99 °C, respectively. (B) Ambient and internal carcass temperatures for shaded site in spring from May 19 (day 0) to July 19 (day 62), 2000. Overall ambient and internal temperature means: 15.44 °C and 18.20 °C, respectively.

grass took on the characteristic burned appearance of black putrefaction (Fig. 2A). Some skin began to separate from bone, most commonly in the shoulder region and limbs. Full deflation of carrion in both habitats was highly variable, occurring between days 22 and 30. Near the end of active decay, the odor of decomposition had changed to a smell characteristic of putrid organ fluids.

During the active decay stage, ambient temperatures reached an average of 16.4 °C at the sun-exposed site and 14.5 °C at the shaded site (Table 1). Internal carcass temperatures averaged 27.4 °C at the sun-exposed site, often reaching over 25 °C over ambient. Alternatively, internal carcass temperatures reached an average of 20.5 °C in the shaded carrion, explaining the slower rate of larval development.

Table 1
Summary of decompositional characteristics by stage of decay and associated ambient and internal carcass temperatures and precipitation in spring

Decay stage	Defining characteristics of decompositional stages	Habitat	Days postmortem	Temperatures (°C)[a]				Precipitation (mm)
				Ambient temperature range	Ambient temperature avg.	Internal temperature range	Internal temperature avg.	
Fresh	No odor; algor mortis; rigor mortis; fresh appearance	Sun Shade	0–1 0–2	5.0–30.4 6.2–31.7	15.2 14.8	9.3–27.5 11.3–28.9	17.3 16.8	0.4
Bloated	Bloating, initiating in abdomen; livor mortis; discoloration; maggots developing inside body openings; moderate odor	Sun Shade	2–12 3–15	1.3–31.4 1.0–25.1	15.5 12.8	4.9–38.1 6.1–19.9	18.5 12.7	11
Active decay	Release of gases, associated with maggot infestation outside of body; liquefaction of tissues; strong odor of decay; black putrefaction; prepupal migration; continual deflation; Skin separation from bone; First pupae near end of stage	Sun Shade	13–30 16–35	−2.8–36.2 4.7–29.0	16.4 14.5	6.0–38.1 8.7–38.3	27.4 20.5	38
Advanced decay	Removal of flesh at extremities (head, limbs, anus); odor moderate, resembles smell of dried organ tissue; dehydration of remaining tissues; bone exposure evident at extremities	Sun Shade	31–42 36–45	3.2–38.4 6.2–29.6	18.6 16.7	18.4–38.1 10.7–28.7	33.2 18.5	8.8
Dry	Little to no odor; hardened, dried, and wrinkled skin; exposed bone and tissue remnants whitish-grey	Sun Shade	42 to >63 46 to >63	4.0–38.4 5.1–32.6	20.4 17.6	11.6–38.1 7.9–36.5	25.5 19.7	72

[a] Temperatures above 37 °C were recorded by the data loggers. However, these temperatures exceed the accurate range of the data loggers and thus should be interpreted with caution.

Characteristics of advanced decay have typically included the removal of most flesh, a decrease in odor, and migration of prepupal larvae from the carrion [1,5]. All of these characteristics marked the advent of advanced decay in both habitats in spring, with the exception of larval migration (Table 1). Prepupal larvae were more common in active decay, although waves of migration were observed over several weeks, starting from day 18 in sun-exposed carcasses and day 20 in shaded carcasses.

Day 30 marked the end of the active decay stage and the beginning of the advanced decay stage for sun-exposed carcasses. Two of the shaded carcasses reached advanced decay by day 35. Skunk kittens (*Mephitis mephitis* (Schreber)) constantly attacked the third shaded carcass. Initially, the skunks preyed on the insects, thereby slowing decomposition. By day 38, the skunks had reduced the majority of visible insects and began to attack the flesh of the carcass, which hastened the rate of decomposition. Thus, by day 39, this slower shaded carcass had reached the advanced decay stage and the same level of decomposition as the other shaded carrion.

The loss of skin on the head, limbs, and posterior was common to all carcasses. However, carrion retained most skin in the abdominal area (Fig. 2B). Remaining hair and skin rapidly dehydrated in the advanced decay stage. Clothing was covered in pupae by the start of this stage and became hard from the drying of decompositional fluids. Cranial and limb bones were exposed on all carcasses and one carcass in each habitat also had the ribs partially exposed.

Ambient temperatures in both habitats increased during the advanced decay stage as the summer season approached. At the sun-exposed site ambient temperatures averaged 18.6 °C, nearly 2 °C higher than the shaded average of 16.7 °C (Table 1). Sun-exposed internal carcass temperatures peaked during this stage and ranged from 38.1 °C to 18.4 °C, with an

Fig. 2. (A) Sun-exposed carcass in active decay in spring (day 20). (B) Shade carcass in advanced decay in spring (day 43). (C) Sun-exposed carcass in dry stage in spring (day 56).

average of 33.2 °C. Internal temperatures may have been higher than the maximum recorded temperature as the accurate upper range of the data logger was 37 °C. However, maggot mass temperatures measured with a hand thermometer ranged from 27 °C to 37 °C during this period. Shaded internal carcass temperatures decreased from the peak experienced in active decay and ranged from 28.7 °C to 10.7 °C, with an average of 18.5 °C.

The final stages of decomposition in spring in Saskatoon best follow the stages of Payne [1], separating final decay into two stages: dry and remains. This experiment however, did not last long enough to observe the remains stage. The rapid desiccation of the carcass, warmer ambient temperatures and lack of precipitation hastened the advent of the dry stage. The carcasses became so dry as to preserve the remaining outer skin and tissue. Under the hardened skin a dark brown sludge was all that remained of the tissues. Heavy rainfall in the beginning of July prevented the sludge from drying out and provided a remnant breeding ground for insects. The outer skin and clothing did not moisten from the rain, remaining crusty and rigid.

By day 41, one exposed carcass was completely dehydrated. All remaining skin had a cheesecloth-like appearance. By day 43, all sun-exposed carcasses were dried. The remaining skin on the abdomen resembled parchment paper and took on a wrinkled, mummified appearance (Fig. 2C). The carcass remnants began to turn a whitish-grey color. By day 46, all shaded carcasses had reached the dry stage. Generally, shaded carcasses retained more abdominal skin than sun-exposed carcasses. Between day 45 and 63, the final day of the experiment, there were few changes in the overall appearance of the carcasses.

3.1.3. Insect succession

Succession tables for forensically significant insects for sunlit and shaded carrion are depicted in Tables 2 and 3, respectively. Most carrion experienced fly activity immediately after placement and all pigs experienced activity within 4 h of death. Oviposition was not observed immediately, but eggs were detected on carcasses the following day, and were likely deposited on day 0, as light rain and overcast skies limited fly activity on day 1. The blow fly *Cynomya cadaverina* (Robineau-Desvoidy) was the most abundant fly attracted to carcasses in both habitats on day 0. Both *Phormia regina* (Meigen) and *Protophormia terraenovae* (Robineau-Desvoidy) were also collected from shaded carrion during the fresh stage.

Table 2
Occurrence matrix of forensically important insects collected from sunlit pig carrion in spring

	Days Postmortem	0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52	54	56	58	60	62
Family	**Genus and Species**	F	Bloat						Active									Advanced						Dry									
Calliphoridae	*Cynomya cadaverina*	a	a	a	a	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Protophormia terraenovae	e	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	a^t	a^t	a	a	a,a^t	a	a	a	a	a	a
	Phormia regina	e	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	a^t	a^t	a	a	a	a	a	a	a	a	a	a
	Lucilia sericata	0	0	a	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Calliphora vicina	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	a	0	a	0	0	0
	Lucilia illustris	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Cochliomyia macellaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	a	0	0	0	0	0	0
Sarcophagidae	*Sarcotachinella sinuata*	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthomyiidae	*Hydrophoria sp.*	a	a	a^g	a^g	a^g	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Muscidae	*Phaonia sp.*	a	a	a	a	a	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Hydrotaea sp.	0	0	0	0	a	a	a	a	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Musca sp.	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Fannia sp.	0	0	0	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Morelia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	a	a	0	0	0	0	0	0	0
Heleomyzidae	*Tephrochlamys sp.*	0	0	0	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Phoridae	*Megaselia sp.*	0	0	a	0	a	a	0	0	0	0	0	0	0	a	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Anevrina sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piophilidae	*Piophila casei*	0	0	0	0	0	a	a	a	a	a	a	a	a	a	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	not identified	0	0	0	0	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphaeroceridae	*Leptocera wirthi*	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sepsidae	*Sepsidimorpha sp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	0	a	0	0	0	0	0	0	0	0	0	0	0
Silphidae	*Thanatophilus lapponicus*	0	a	a	a	a	a	a	a	a	a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l	l	l	l	l	l
	Heterosilpha ramosa	0	0	0	0	0	0	0	0	0	0	0	0	a	a	a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l	l	l	l	l	l	l	l	l	l
Staphylinidae	*Creophilus maxillosus*	0	0	0	0	0	0	0	0	a	a	a	a	a	a	a	a	l	l	l	l	l	l	l	l	l	l	l,a	l	l	l	l	l
	Lobrathium sp.	0	0	0	0	0	0	0	a	a	a	a	a	a	a	a	a	a	a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a
Scarabaeidae	*Phanaeus sp.*	0	0	0	a	0	0	0	0	a	a	a	a	a	a	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Aphodius sp.	0	0	0	0	0	0	a	0	0	0	0	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Histeridae	*Saprinus distinguendus*	0	0	0	0	0	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
	Hister furtivus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0
Nitidulidae	*Carpophilus sp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0	a	a	a	a	a	a	a	a	a
Cleridae	*Necrobia rufipes*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	a	a	a	a	a
Dermestidae	*Dermestes maculatus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	l	0	0	0

Light shading indicates very low and/or inconsistent numbers of individuals collected across all three carcasses. Dark shading indicates consistent and predictable occurrence of individuals. Abbreviations: F = Fresh, a = adults, a^t = teneral adults, a^g = adult gravid females, p = pupae, l = larvae, e = eggs.

Table 3
Occurrence matrix of forensically important insects collected from shaded pig carrion in spring

	Days Postmortem	0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52	54	56	58	60	62
Family	**Genus and Species**	Fresh		Bloat						Active										Advanced					Dry								
Calliphoridae	*Cynomya cadaverina*	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a,a^t	a,a^t	a,a^t	a	0	0	0	0	0	0
	Protophormia terraenovae	e,a	e,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,a^t	l,a^t	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a
	Phormia regina	e,a	e,a	l	l	l	l	l	l	l,a	l,a	l,a	l,a	l,a	l,a	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	a^t	a	0	0	0	0
	Lucilia illustris	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0
	Lucilia silvarum	0	0	0	0	0	0	0	a	0	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sarcophagidae	*Liopygia sp.*	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Muscidae	*Phaonia sp.*	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Morellia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	a	a	a	a	0	0	0	0	0	0	0	0	0	0
Anthomyiidae	*Hydrophoria sp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	a	a	a	a	a	a	a	a	0	0	0	0	0	0
Heleomyzidae	*Tephrochlamys sp.*	0	0	0	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	0	0	0	0	0	0	a	0	0	0	0	0	0	0
Phoridae	*Phora sp.*	0	0	a	a	0	a	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Anevrina sp.	0	0	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	0	0	0	0	0	0
	Megaselia sp.	0	0	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piophilidae	*Piophila casei*	0	0	0	0	0	0	0	0	0	0	0	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a,l	l	l	l
Sphaeroceridae	*Leptocera wirthi*	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sepsidae	*Sepsidimorpha sp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0
Chloropidae	not identified	0	0	a	0	0	0	0	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Silphidae	*Thanatophilus lapponicus*	0	0	0	a	a	a	a	a	a	a	a	a	a	a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a
	Oeceoptoma noveboracense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	l	l	0	0	a	0	0	0	0	0	0
	Heterosilpha ramosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	l	0	0	0	0	0	0	0	0	0
Staphylinidae	*Lobrathium sp.*	0	0	0	0	0	a	0	0	a	a	a	a	a	a	a	a	a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a
	Creophilus maxillosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	l	l	l	l	l	l	l	l	l	l	l	l	l	l	l
Scarabaeidae	*Aphodius sp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Saprinus distinguendus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	0	0	0	0
	Hister furtivus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	a	a	a	a	a	a	0	0	0
Nitidulidae	*Carpophilus sp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	a	a	a	0	0	0	0	0	0	0	a	0	0	0	0	0	0
Cleridae	*Necrobia rufipes*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a

Light shading indicates very low and/or inconsistent numbers of individuals collected across all three carcasses. Dark shading indicates consistent and predictable occurrence of individuals. Abbreviations: a = adults, a^t = teneral adults, p = pupae, l = larvae, e = eggs.

In both habitats, the bloated stage attracted a greater diversity and number of insects (Tables 2 and 3). However, the calliphorids remained the most numerous flies in both habitats. The blow flies *P. regina* and *P. terraenovae* were by far the most common flies feeding and ovipositing on the sun-exposed carrion. At shaded carrion, adult *C. cadaverina* and *P. terraenovae* were the most abundant. The difficulty in identifying immature stages of blow flies forced the majority of larval identification to come from reared adults. In both habitats, several larvae were collected from various areas. However, the only two species that emerged from laboratory rearing of spring collections were *P. regina* and *P. terraenovae*. It is possible that the rearing technique could have favored the development of calliphorid flies over that of other Dipteran species. Another possibility is strong interspecific competition where the greatest competitors in spring are *P. regina* and *P. terraenovae*.

The blow flies *Lucilia illustris* (Meigen), *Lucilia sericata* (Meigen) and *Lucilia silvarum* (Meigen) made their first appearances during the bloated stage, but were uncommon visitors. Flesh flies (Sarcophagidae) were almost exclusively captured near the carcass, but not on the carcass proper. The muscid fly *Hydrotaea* Robineau-Desvoidy and the anthomyiid fly *Hydrophoria* Robineau-Desvoidy were common visitors only to sun-exposed carrion. Other dipterans appearing in the bloated stage included members of Sarcophagidae, Piophilidae, Phoridae, Heleomyzidae, and Chloropidae (Tables 2 and 3).

The elusive carrion beetle, *Thanatophilus lapponicus* (Herbst) (Silphidae), was first collected on day 2 from sun-exposed carrion and day 5 from shaded carrion. During the bloated stage, *T. lapponicus* was the most abundant coleopteran in both habitats. This was the only beetle that had a predictable arrival time during the bloated stage.

In the active decay stage, the heads of all carcasses were entirely infested with calliphorid larvae in varying stages of development. Although *Piophila casei* (Linnaeus) was first collected in the bloated stage, their numbers increased dramatically in the active decay stage in both habitats. The number of adult blow flies visiting the carcass was also greatest during this stage. By day 20, huge maggot masses were evident in several areas of the sun-exposed carcasses. Maggot mass temperatures taken with a hand thermometer ranged from 35 °C to 38 °C. Day 20 was also the first day that pupae were observed at the sun-exposed carrion. These trends occurred on day 21 in shaded carrion.

The number of coleopterans increased considerably during the active decay stage. The first larval carrion beetles (Silphidae) were collected on day 20 and day 28 at sun-exposed and shaded carrion, respectively (Tables 2 and 3). The silphid *Heterosilpha ramosa* (Say) was restricted to the sun-exposed carrion, while *T. lapponicus* was found in both habitats. Adult rove beetles (Staphylinidae) made their first appearance at the sun-exposed carrion on day 18 and began to rival the numbers of Silphidae. The shaded carrion also experienced a major increase in the number of adult Staphylinidae, starting from day 16. Immature Staphylinidae were first collected on day 35 on shaded carrion, the last day of active decay. However, the presence of larval Staphylinidae was more characteristic of advanced decay for both habitats.

There was more diversity in species of coleopterans at the sun-exposed sites. The number of scarab (Scarabaeidae) and clown beetles (Histeridae) was also greater at the sun-exposed sites. The histerid beetles were not collected from shaded carrion during this stage and the Scarabaeidae were infrequent visitors. The sap beetles (Nitidulidae) made their first appearance during this stage on day 27 and 30 at the shaded and sun-exposed sites, respectively.

From day 31 to 41 of the advanced decay stage, fly activity decreased in both habitats. At the sun-exposed sites, there were no adult blow flies collected until day 41, when the first major adult emergence occurred. Laboratory rearing of immature specimens collected from sun-exposed carrion were identified as *P. regina* and *P. terraenovae*. On day 41, there was hundreds of newly emerged *P. regina* near every sun-exposed carcass.

Another wave of fly emergence occurred on day 43 at the sun-exposed carrion. Flies from this wave were identified as *P. terraenovae*. At shaded carrion, the first major emergence of adult flies occurred between days 43 and 45. Flies collected included *C. cadaverina* and *P. terraenovae*. Thus, immature *C. cadaverina* must have been present on shaded carrion, even though they were never identified from larval specimens or adults emerging from laboratory rearing. During the advanced decay stage, *P. casei* disappeared from sun-exposed remains, but increased dramatically at shaded remains.

Immature Silphidae and Staphylinidae were very common in both habitats during the advanced decay stage. The number of scarabs remained abundant at the sun-exposed sites but disappeared from shaded carrion. The histerid beetle *Saprinus distinguendus* Marseul remained relatively abundant at sun-exposed carrion. Only one histerid beetle, *Hister furtivus* LeConte was collected from a shaded carcass on day 45. The Histeridae were more common in the dry stage at shaded carrion.

Insect diversity increased during the dry stage, especially at the sun-exposed carcasses (Table 2). The blow fly *Cochliomyia macellaria* (Fabricius) was collected for the first time at sun-exposed carrion. This species is known to have a more southern distribution and only flies north during summer months [19,21]. This marks the first record of *C. macellaria* in Saskatchewan. New fly emergence on day 50 released a new wave of *P. terraenovae* on sun-exposed carcasses.

Coleopterans were the dominant insects during the dry/remains stage. Larval staphylinids and silphids remained abundant in both habitats. The histerid beetle *S. distinguendus* finally made its appearance on shaded carrion on day 56. At sun-exposed sites, *S. distinguendus* remained abundant throughout the dry stage. The histerid *H. furtivus* was unique to the shaded carrion and increased in abundance during the dry stage. The red-legged ham beetle, *Necrobia rufipes* (DeGeer), made its first appearance on day 50 and 52 in the shaded and sun-exposed habitats, respectively. The only dermestid beetle collected was one larva of *Dermestes maculatus* from a sun-exposed carcass on day 56. Final collections were made on day 62.

3.2. Summer experiment

3.2.1. Temperature data

Ambient temperature readings for summer for both the sun-exposed and shaded sites are presented in Fig. 3. In contrast with the spring experiment, there was no significant difference between the means of the two treatments ($p = 0.01$). The sun-exposed site had an average temperature of 19.5 °C throughout the experiment, whereas the shaded site experienced an average temperature of 19.1 °C. Daily maximums were similar in both habitats, whereas daily minimums were lower at the sun-exposed site.

Mean internal carcass temperatures for summer are also depicted in Fig. 3. There was a significant difference between the means of these two treatments ($p = 0.01$). Interestingly, carrion at the shaded sites experienced a 3.9 °C higher average internal temperature than sun-exposed carrion. From day 0 to day 4, internal temperatures were nearly identical in both habitats. From day 5 to day 10, the data logger in the shaded carcass registered temperatures over 38 °C, which exceeded the accuracy limits of the data logger. The sun-exposed carcass also had recorded temperatures up to 38 °C on days 6 and 7. Thus, temperatures during these periods cannot be ascertained with accuracy. However, maggot mass temperatures recorded with a hand thermometer ranged from 33 °C to 41 °C, with the highest temperatures recorded from masses in the direct sun on the sun-exposed carcass. From day 8 onward, sun-exposed carrion experienced a decline in internal temperatures with large daily fluctuations. A similar pattern occurred after day 10 in shaded carrion, although internal carcass temperatures remained higher than average daily ambient temperatures.

3.2.2. Decomposition

The defining characteristics of each stage of decay, along with the associated ambient and internal carcass temperature readings are summarized in Table 4.

Decomposition occurred at a significantly faster rate in summer due to the higher ambient temperatures. Carcasses in both habitats exhibited bloating on day 1.

There were very few differences in decomposition between the sun-exposed and shaded carcasses. By day 2, all carcasses were significantly bloated in all body regions. Rigor mortis initiated on day 1 and evidence of hypostasis was clearly evident by day 2. By day 4 the bloat was so severe that the organs burst through the abdominal wall. The carcasses expanded to twice their original size and filled the entire cage. Skin started to exhibit the characteristic blue-green marbling from gaseous build-up in the abdomen. Abdominal distension pushed clothing against the shoulders and neck of the pigs.

On day 5, the abdominal wall, thoracic region, anus, genitals, and orifices of the head of all carcasses ruptured, spilling developing larvae and decompositional fluid. The carcasses did not deflate upon rupture. Day 5, however, is considered to be the first day of active decay due to the rupturing of the skin, the release of decompositional fluids, gas and subsequent froth, and the associated putrid odor (Table 4).

During active decay, the edges of broken skin blackened from putrefaction and started to flake from maggot activity. By day 5, deflation initiated in the head, neck, and exposed organs of carcasses in both habitats. At this point, maggots had infested every region of the carcasses. By day 7, deflation had extended to the abdomen and buttocks. Full deflation occurred by day 9. The sun-exposed pig carrion started to attract numerous vertebrate scavengers, which were not deterred by the cages and mesh underlay. By day 7, every sun-exposed carcass displayed some evidence of scavenging. However, the animal responsible was likely quite small and concentrated on removing flesh from the distal ends of the forelimbs. Shaded carrion displayed almost no evidence of scavenging throughout the summer experiment.

By day 7, the skin of the sun-exposed carcasses started to dehydrate from the intense heat and exhibited an orange-brown discoloration. Similar events took place on shaded carrion by day 8, although the moisture level remained higher compared to sun-exposed carrion. Between the maggot activity and the high ambient temperatures, the sun-exposed carcasses were rapidly diminishing as a resource for insects. Maggots began to retreat to the underside of carrion, under clothing, and into the internal cavities where moisture was still available. As shaded carcasses were protected from direct sunlight, the larvae were able to continue feeding all over the body for an extended period of time. The skin of shaded carcasses also remained pliable and damp longer. Cranial exposure was evident on most carcasses by day 7.

The active decay stage occurred during the hottest days of summer. The average ambient temperature was approximately 23 °C in both habitats, with daily highs over 38 °C (Fig. 3 and Table 4). Internal carcass temperatures also peaked during the active decay stage. At the shaded site, internal temperatures never dropped below 27.8 °C, as maggot activity continued feverishly throughout this stage. The sun-exposed carrion experienced a 4.5 °C lower internal temperature than shaded carrion, averaging 32.9 °C. The rapid desiccation of the sun-exposed carrion led to the early departure of underdeveloped larvae. Thus, maggot mass heat generation declined by day 8 and internal temperatures began to approximate ambient.

At the shaded sites, drops in internal carcass temperature were consistent with the mass migration of post-feeding larvae. Mass migration first occurred on day 10 at shaded sites, but was not observed until day 12 at sun-exposed sites. Core maggot mass temperatures at the sun-exposed site ranged from 40 °C to 43 °C. At shaded sites, core temperatures ranged from 34 °C to 37 °C. The high temperatures at the sun-exposed site likely exceeded the maximum threshold for most species, causing a slower rate of development. This was confirmed by the presence of heat stressed and dead larvae at the sun-exposed sites.

Advanced decay started on day 12 in both habitats. The stench of decay had decreased and changed to a dried, charred odor. Waves of calliphorid larval migration continued on day 12. At sun-exposed carcasses, many larvae were leaving the carcass in search of lower temperatures. Several non-post-feeding, 3rd instar larvae were found underneath the grass away from the carcass. The grass provided protection from the intense heat, as the temperature was 4–5 °C cooler than the skin

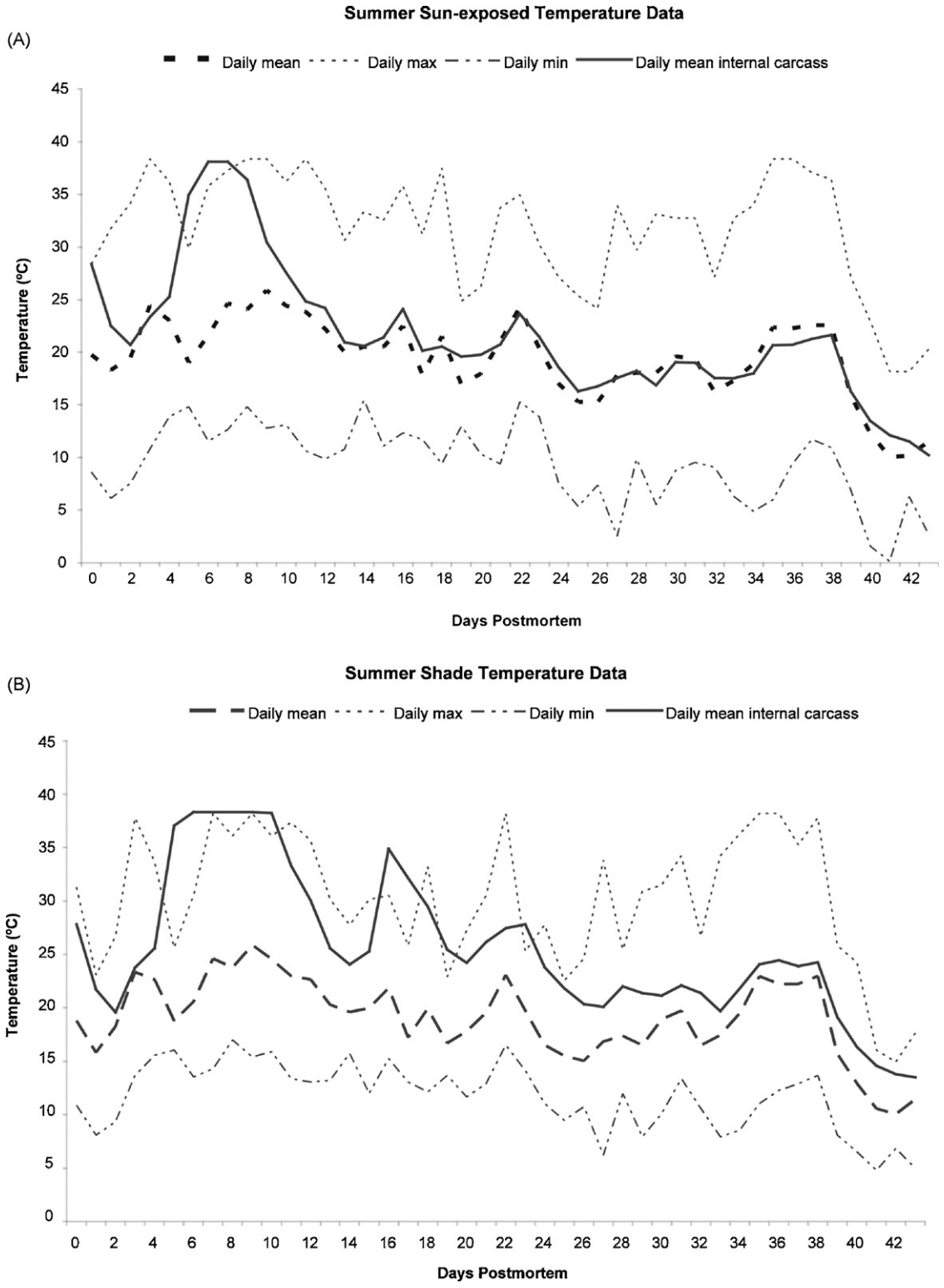

Fig. 3. Summary of temperatures recorded in the summer experiment. Accurate temperature range of data loggers was −5 °C to 37 °C (±0.1 °C accuracy/resolution). (A) Ambient and internal carcass temperature for sun-exposed site in summer from July 19 (day 0) to August 31st (day 43), 2000. Overall ambient and internal temperature means: 19.47 °C and 21.56 °C, respectively. (B) Ambient and internal carcass temperature for shaded site in summer from July 19 (day 0) to August 31st (day 43), 2000. Overall ambient and internal temperature means: 19.08 °C and 25.50 °C, respectively.

temperature of the carrion. The extent of carcass desiccation was greater at the sun-exposed sites and left maggots scrambling for an alternative food source. By day 14, more flies and larvae were found dead near the sun-exposed carrion.

Shaded carrion in the advanced decay stage experienced a dramatic decline in insect activity. Developing larvae were not readily visible, although they may have withdrawn to areas underneath or deep within the carcasses. The surrounding soil

Table 4
Summary of decompositional characteristics by stage of decay and associated ambient and internal carcass temperatures and precipitation in summer

Decay stage	Defining characteristics of decompositional stages	Habitat	Days postmortem	Temperatures (°C)[a]				Precipitation (mm)
				Ambient temperature range	Ambient temperature mean	Internal temperature range	Internal temperature mean	
Fresh	No odor; algor mortis; fresh appearance	Sun Shade	0 0	8.6–28.4 10.9–31.3	19.8 18.8	20.7–34.1 19.7–34.3	28.4 27.8	0
Bloated	Bloating, increasing through stage;; rigor mortis; livor mortis; discoloration; maggots teeming inside body openings; moderate odor	Sun Shade	1–4 1–4	6.1–38.4 8.1–37.8	21.3 20	17.3–29.7 17.3–34.9	23 22.7	0
Active decay	Rupture of abdominal wall; complete larval infestation; lquefaction of tissues; strong, putrid odor, black putrefaction; prepupal migration; deflation initiating at extremities, completed half-way through stage; skin dehydration and discoloration from heat (dark orange-brown)	Sun Shade	5–11 5–11	10.6–38.4 13.4–38.2	23.4 23	14.1–38.1 27.8–38.3	32.9 37.4	10.8
Advanced decay	Removal of flesh at extremities (head, limbs, anus); odor moderate, resembling smell of burnt skin; skin completely dehydrated with signs of mummification; bone exposure evident at extremities; larval migration continuing, decrease in insect activity	Sun Shade	12–25 12–25	5.4–37.5 9.5–38.2	19.9 19.3	7.4–36.4 20.36–38.3	20.6 26.8	49.6
Dry/remains	Odor negligible, resembling smell of charred skin; remaining skin brittle and rigid; skin easily separated from bone	Sun Shade	26 to >43 26 to > 43	0.1–38.4 4.8–38.2	17.2 17.2	2.1–37.5 11.5–31.7	17.1 20.2	3

[a] Temperatures above 37 °C were recorded by the data loggers. However, these temperatures exceed the accurate range of the data loggers and thus should be interpreted with caution.

was sampled for pupae and larvae, but none were found. Post-feeding larvae may have migrated a great distance to areas that were not sampled. Fly activity was extremely low and beetles were rarely sighted. This low activity occurred until day 14, when the first emergence of blow flies occurred. At the sun-exposed sites, the first emergence of adult flies occurred on day 16. The increased fly activity coincided with an increase in beetle activity, especially at the sun-exposed sites.

By day 16, a vast majority of the abdominal skin remained intact, and appeared wrinkled, brittle, and mummified. The complete desiccation of the skin resulted in few changes in the overall appearance of the carrion for the remainder of the experiment. However, vertebrate scavenging continued to occur at sun-exposed carrion, removing more skin and bones as the advanced decay stage progressed.

The beginning of the dry/remains stage in summer was difficult to distinguish from the end of the advanced decay stage. There were no discernible events or gross morphological changes that marked the separation. However, by day 26 the odor of decay was slight at sun-exposed sites, resembling the smell of burnt skin. Approximately 30% of the skeleton was exposed on sunlit carrion, mostly due to scavenging. Remaining skin was extremely brittle and could be easily separated from the skeleton. At the shaded sites, the outer skin remained intact and preserved, although rigid. The odor of decay was negligible. A saw-dust-like residue was observed in

the abdominal region of all carcasses by day 34. Final collections were made on day 43.

3.2.3. Insect succession

Fly activity occurred immediately upon the arrival of the carcasses in the covered flatbed. Oviposition occurred on some carrion before placement on the mesh underlay. Only blow flies were collected on day 0 (Table 5). Fly activity was higher at the sun-exposed sites and three species were collected: *C. macellaria*, *P. regina*, and *L. sericata*. At the shaded site, *C. macellaria* was the only insect collected.

In the bloated stage, *C. macellaria* remained the dominant fly at shaded carrion, followed by *Musca domestica* Linnaeus (Muscidae). There was a greater diversity of flies at the sun-exposed carrion, which additionally attracted *P. regina*, *L. sericata*, and *Agria housei* (Shewell) (Sarcophagidae). At both habitats, *P. casei* arrived at the end of the bloated stage on day 4. Although all of these flies were collected in the near vicinity of the carrion, only the blow flies were actually observed on the carrion proper. By day 2, the carrion beetles *H. ramosa* and *T. lapponicus* were collected from sun-exposed and shaded carrion, respectively. By day 3, maggot masses had developed on various locations of the carcasses.

Table 5
Occurrence matrix of forensically important insects collected in summer from, (A) sunlit pig carrion; (B) shaded pig carrion

A

Days Postmortem		0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42
Family	**Genus and Species**	F	Bloat		Active			Advanced							Dry								
Calliphoridae	*Cochliomyia macellaria*	a	l,a	l,a	l,a	l,a	l,a	l,p	l,p	p	0	0	0	0	0	0	0	0	0	0	0	0	0
	Phormia regina	a	l,a	l,a	l,a	l,a	l,a	l,p	l,p	a	a	a	a	a	a	a	a	a	0	0	0	0	0
	Lucilia sericata	a	a	a	l	l	l	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sarcophagidae	*Agria housei*	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Muscidae	*Musca domestica*	0	a	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Morelia sp.	0	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Hydrotaea sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0
Piophilidae	*Piophila casei*	0	0	a	a	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Parapiophila sp.	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phoridae	*Megaselia sp.*	0	0	0	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sepsidae	*Meroplius stercorarius*	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Silphidae	*Thanatophilus lapponicus*	0	0	0	a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a
	Heterosilpha ramosa	0	a	0	0	0	0	a	a	a	a	a	a	a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a
Nitidulidae	*Carpophilus sp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	a	a	a	a	a	a	a	a	a

B

Days Postmortem		0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42
Family	**Genus and Species**	F	Bloat		Active			Advanced							Dry								
Calliphoridae	*Cochliomyia macellaria*	a	l,a	l,a	l,a	l,p	l,p	l,p	l,p	p	p	0	0	0	0	0	a	0	0	0	0	0	0
	Calliphora vicina	0	0	0	0	a	0	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0	0
Muscidae	*Musca domestica*	0	a	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Morelia sp.	0	0	0	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Hydrotaea sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0
Piophilidae	*Piophila casei*	0	0	a	a	a	a	a	a	a	a	a	l,a	l	l	0	0	0	0	0	0	0	0
Phoridae	*Megaselia sp.*	0	0	0	0	0	0	0	0	a	a	0	0	0	0	0	0	0	0	0	0	0	0
	Phora sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a
Sepsidae	*Sepsidimorpha sp.*	0	0	0	0	0	0	0	0	a	0	0	0	0	0	a	0	0	0	0	0	0	0
Silphidae	*Thanatophilus lapponicus*	0	a	a	a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a
Staphylinidae	*Creophilus maxillosus*	0	0	0	0	0	0	0	0	l	l	l	l	l	l	l	l	l	l	l	l	l	l
	Lobrathium sp.	0	0	0	0	0	0	0	a	l,a	l	l	l	l	l	l	l	l	l	l	l	l	l
Cleridae	*Necrobia rufipes*	0	0	0	0	0	0	0	0	0	0	0	0	0	a	a	a	a	a	0	0	0	0
Nitidulidae	*Carpophilus sp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	a	a	a	a
Histeridae	*Hister furtivus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	0	a	0	0	0

Light shading indicates very low and/or inconsistent numbers of individuals collected across all three carcasses. Dark shading indicates consistent and predictable occurrence of individuals. Abbreviations: F = fresh, a = adults, p = pupae, l = larvae, e = eggs.

The active decay stage was characterized by an increased diversity of dipteran colonizers, especially at the exposed sites. On day 6, new arrivals at the sun-exposed sites included *Megaselia* Rondani (Phoridae), *Parapiophila* McAlpine (Piophilidae), and *Meroplius stercorarius* (Robineau-desvoidy) (Sepsidae). At the shaded sites, *Morellia* Robineau-desvoidy (Muscidae) and *C. vicina* arrived on day 6 and day 8, respectively. Larval identifications demonstrated the presence of immature *C. macellaria* in both habitats, and immature *L. sericata* and *P. regina* at the sun-exposed sites. However, *L. sericata* was not identified from laboratory rearing of larvae. The number of adult *P. casei* and *M. domestica* also increased in the active decay stage in both habitats. Immature and adult *T. lapponicus* remained the only coleopterans to colonize the remains during this stage. Immature silphids first appeared on day 8 in both habitats.

In the advanced decay stage the diversity of insects decreased dramatically (Table 5). Daily maximum temperatures were often above 30 °C, approaching as high as 38 °C (Table 4). Many of the developing dipteran larvae were showing signs of heat stress. The rapid depletion of the carrion would have made competition for resources intense. Immature *P. casei* were abundant at the shaded sites, and larvae were observed jumping in the characteristic spring-like manner for this species. Interestingly, the dominant blow fly larvae differed between shaded and sunlit carrion during this stage. At the shaded carcasses *C. macellaria* dominated, while *P. regina* was in the majority at the sun-exposed carrion.

Coleopterans were restricted to carrion beetles on the sun-exposed carcasses during the advanced decay stage. Both adult and larval *H. ramosa* and *T. lapponicus* were collected from sun-exposed carrion. The return of *H. ramosa* occurred on day 12 and larvae of this species were collected on day 26. On day 14, adult Staphylinidae were first collected on shaded carrion. Immature Staphylinidae were collected on day 16 and included larvae of *C. maxillosus*. Although adult *C. maxillosus* were never collected in summer, their offspring confirm their presence. Due to the high daily temperatures in summer, it is likely that adults were hidden underneath or deep within the carcasses. Compared to spring, the advanced decay stage in summer had a very low diversity of coleopteran species. Many underdeveloped fly larvae were either dying or leaving the carcass for a new resource, and may account for the lack of predaceous beetles. Additionally, many of the sun-exposed carrion had been partially scavenged during this stage and may also account for the lowered diversity.

In the dry/remains stage, beetles increased in number and diversity. Clerids were the first newcomers at the shaded site, arriving on day 26. Histerids appeared on day 32 at the shaded sites, but were never abundant. Sap beetles (Nitidulidae) first arrived on day 26 and day 34 at sun-exposed and shaded carrion, respectively. Interestingly, scarab beetles were never collected from carrion in either habitat. The number of larval Silphidae and Staphylinidae were extremely abundant on carrion in both habitats, feeding on remnant dipteran larvae. These two families remained the dominant coleopterans for the remainder of the experiment.

3.3. Fall experiment

3.3.1. Temperature data

Ambient temperatures in fall exhibited the most daily fluctuation and the lowest mean compared to spring and summer. Ambient and internal carcass temperature readings for the sun-exposed and shaded sites are presented in Fig. 4. The average ambient temperature in both habitats did not differ significantly ($p = 0.01$). Generally, the shaded site demonstrated less fluctuation in temperature than the exposed site, especially in October. In both habitats, the average temperature in September was just above 12 °C, whereas the average temperature in October was just above 5 °C.

The data logger measuring internal carcass temperature at the shaded site was never recovered at the end of the experiment, even after searching the surrounding soil, leaf litter, and the carcass proper. The average internal carcass temperature for the duration of the experiment at the sun-exposed site was 10.0 °C. In September, the average internal temperature was 14.6 °C. Maximum internal temperatures were recorded day 16, after which the internal temperature mimicked ambient. The average internal temperature in October was lower than ambient, averaging 4.5 °C.

3.3.2. Decomposition

Pigs used in the fall experiment were slightly smaller than in previous experiments. However, they remained within the mid-weight range established by Komar and Beattie [17] as the most appropriate size model for human decomposition. However, the smaller pig size may have had an impact on the rate of decay, an effect that was not quantified in this experiment. On day 0, fly activity was abundant and diverse. Flies were seen feeding at the thoracic wound of most carcasses even before placement on the mesh underlay. The rainy, overcast, and cool weather of days 1–4 limited fly activity and bloating. By day 3, a very slight distension was visible in the necks and hernias of sun-exposed carrion. Similar bloating was observed on shaded carrion on day 4. Both ambient and internal carcass temperature readings for each decompositional stage are summarized in Table 6.

Bloating had extended to the remainder of the body by day 4 in sunlit carrion and day 6 in shaded carrion. Carcasses in either habitat never reached the same degree of bloating exhibited in carrion in the previous seasons. There was little disparity between the decomposition of shaded and sun-exposed carcasses from the bloated stage onward. By day 5, the odor of decay remained negligible. Bloating peaked on day 8 and skin discoloration became evident. By day 8, large maggot masses infested all orifices of the body and the artificial thoracic wound.

The first evidence of liquefaction occurred on day 11 and coincided with the initiation of deflation. Maggots had infested the entire head region of the carcasses. In other areas, larvae remained inside the body cavities. A putrid stench was associated with the remains by day 11. One sun-exposed carcass became increasingly scavenged by a variety of animals

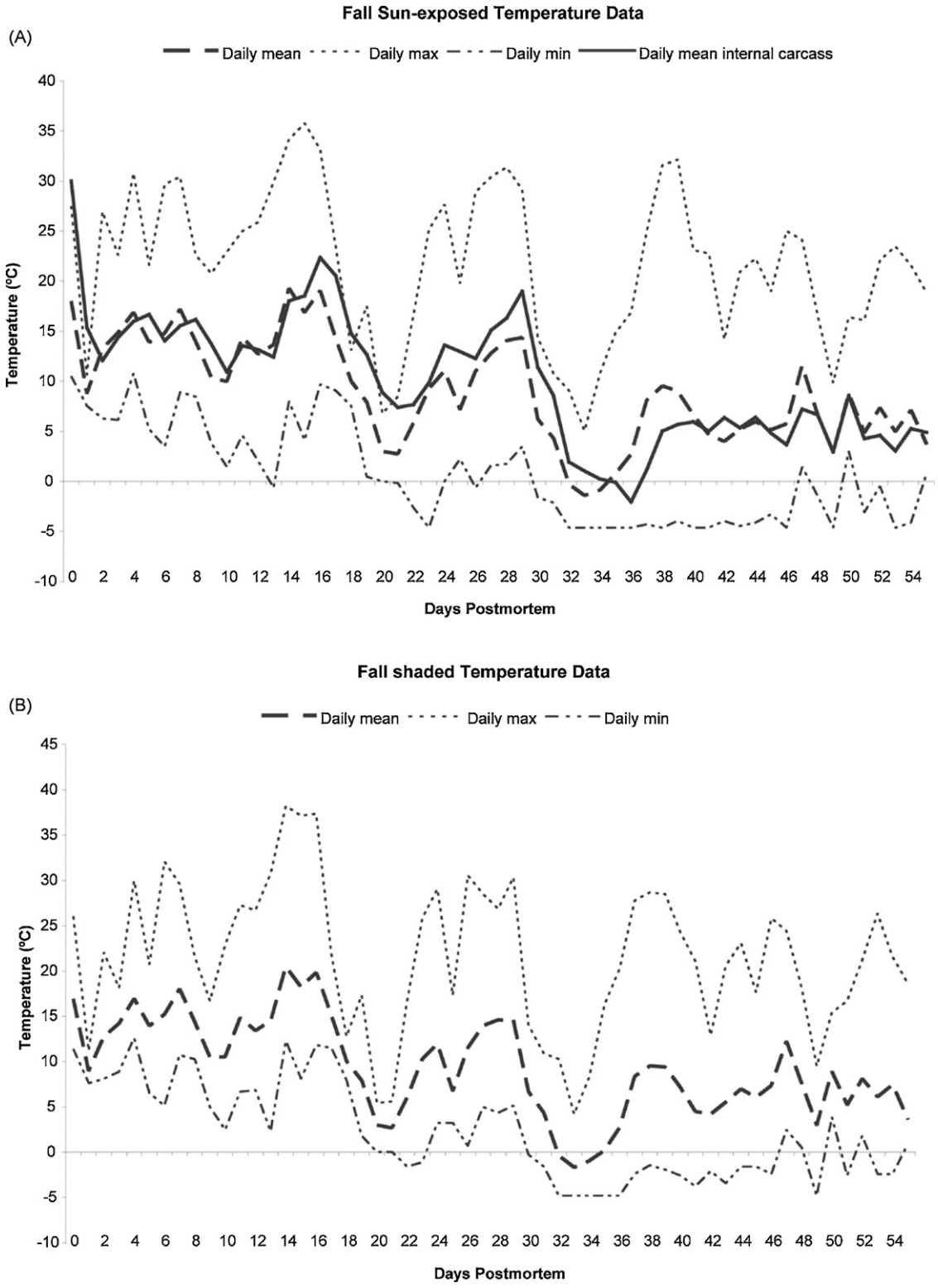

Fig. 4. Summary of temperatures recorded in the fall experiment. Accurate temperature range of data loggers was −5 °C to 37 °C (± 0.1 °C accuracy/resolution). (A) Ambient and internal carcass temperature for sun-exposed site in fall from September 1st (day 0) to October 26 (day 55), 2000. Overall ambient and internal temperature means: 9.0 °C and 10.0 °C, respectively. (B) Ambient temperature for shaded site in fall from September 1st (day 0) to October 26 (day 55), 2000. Overall ambient temperature mean: 9.36 °C.

throughout the experiment. A badger had built a den near the shaded carrion and continually attacked two of the carcasses. The extensive scavenging resulted in variability in the decay rates of these carcasses.

Deflation occurred slowly and varied widely among all of the carcasses. However, all of the pigs were approximately 50% deflated by day 15, and 95% deflated by day 21. By day 17, the skin and surrounding soil blackened and the head, neck, and

Table 6
Summary of decompositional characteristics by stage of decay and associated ambient and internal carcass temperatures and precipitation in fall

Decay stage	Defining characteristics of decompositional stages	Habitat	Days postmortem	Temperatures (°C)[a]				Precipitation (mm)
				Ambient temperature range	Ambient temperature mean	Internal temperature range	Internal temperature mean	
Fresh	No odor; algor mortis; fresh appearance	Sun Shade	0–2 0–3	6.3–27.5 7.6–26.0	12.6 12.8	9.6–36.8 Lost data	17.7 Lost data	13.8
Bloated	Bloating, initiating in anterior region and abdomen; livor mortis; rigor mortis; discoloration; maggots developing inside body openings; moderate odor	Sun Shade	3–10 4–10	1.4–30.8 2.4–32.1	14 14.3	5.6–20.4 Lost data	14.5 Lost data	0.4
Active decay	Rupture of anterior body cavities; strong, putrid odor; slow deflation of body, initiating in anterior regions; black putrefaction; skin dehydration with some mummification later in stage; bone exposure of skull; eventual preservation of body in sub-zero weather	Sun Shade	11 to >54 11 to >54	−4.6–35.8 −4.8–38.2	9.0 9.3	−3.8–36.8 Lost data	8.5 Lost data	7.9

[a] Temperatures above 37 °C were recorded by the data loggers. However, these temperatures exceed the accurate range of the data loggers and thus should be interpreted with caution.

anal regions were overcome with decompositional fluids. All developing larvae had returned to the inner cavities of the carcass and underneath clothing at sun-exposed carcasses. These areas provided protection from the cold September nights. On sunny, warm days, maggots would reappear outside of the cavities. In comparison, the shaded site experienced higher evening temperatures and larvae could still be exposed to air without lethal effects. Thus, larvae at shaded carrion were visible outside of the carcass for a longer period of time.

Beyond day 22, decomposition varied from the typical patterns. The head of the carcasses dehydrated, exposing the cranium. By day 26, the anterior portion of the carcass appeared to be in the advanced decay stage. Meanwhile, putrefaction continued in the abdominal region, producing frothy liquid and further blackening the soil and outer edges of the skin. A mid-ventral seam was created by internal maggot activity where the abdomen met the ground. The remainder of the abdominal skin was intact. By day 31, the outer skin on all of the carcasses had become leathery and hard. Once the skin was dry and rigid, the carcass could virtually be lifted in half at the mid-ventral seam.

On the inside of the carcass, active decay continued at a slow rate, and various larvae were continuing development in the wet tissues. In October (day >30), the cold ambient temperatures slowed decay to a near halt. The average temperature in October was approximately 5 °C in both habitats. Evening frost was also a common occurrence in October. Between day 31 and day 54 there were few overall changes in the appearance of the carrion. Final collections were made on day 54.

Due to the continual decrease in ambient temperatures in the fall experiment, decomposition followed a unique pattern. During the observational period of the experiment, the carcasses progressed through only three stages of decay. The characteristics of these stages are summarized in Table 6. Carcasses continued in active decay stage from day 11 onward, although decomposing at an extremely slow rate.

3.3.3. Insect succession

Fly activity was observed immediately after placement of the carrion. Blow flies were feeding at all of the orifices and the thoracic wounds. Days 1–3 were cold and rainy and severely limited fly activity. Oviposition was first observed on day 2. There was a greater diversity of flies attracted to the carrion in the fresh stage compared to other seasons (Table 7). At the sun-exposed site, *C. macellaria*, *C. cadaverina*, *P. regina* and *Lucilia caeruleiviridis* (Macquart) were collected. At the shaded site, *C. macellaria*, *L. illustris*, and *L. caeruleiviridis* were collected.

The bloated stage coincided with the arrival of several new species. On day 4, *T. lapponicus* was collected from the sunlit carrion and on day 5, *H. ramosa* was collected at the shaded carrion. Adult Staphylinidae were also collected on day 4 at the sunlit site. Members of Phoridae and Muscidae arrived at sunlit carrion on day 4 and day 8, respectively. The blow fly *L. illustris* and the cheese skipper *P. casei* arrived on day 11 at sunlit carrion. There was far less diversity in insects at the shaded site; silphid beetles were the only new insect to arrive during the bloated stage.

Table 7
Occurrence matrix of forensically important insects collected in fall from, (A) sunlit pig carrion; (B) shaded pig carrion

A

Days Postmortem		0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52	54
Family	**Genus and Species**	Fresh		Bloat				Active																					
Calliphoridae	*Cochliomyia macellaria*	a	a	l,a	l,a	l,a	l,a	l.a	l,a	l,a	l,a	l,a	l,p	l,p	l,p	l,p	l	l,a	l	l	l	l	l	l	l	l	l,p	l,p
	Phormia regina	a	a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l	l	l,p	p	p	p	0	0	0	0	0	0	0	0	0	0	0	0	0
	Lucilia coeruleiviridis	a	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Cynomya cadaverina	0	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Lucilia illustris	0	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Calliphora vomitoria	0	0	0	0	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Calliphora vicina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0
	Lucilia sericata	0	0	0	0	0	0	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Muscidae	*Morelia sp.*	0	0	0	0	a	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Hydrotaea sp.	0	0	0	0	0	0	0	0	0	0	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	not identified	0	0	0	0	0	0	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piophilidae	*Piophila casei*	0	0	0	0	0	0	a	a	a	a	a	a	a	a	a	a	a	a	a	a	0	0	0	0	0	0	0	0
	Parapiophila sp.	0	0	0	0	0	0	0	0	0	a	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phoridae	*not identified*	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Silphidae	*Thanatophilus lapponicus*	0	0	a	a	a	a	a	a	a	a	a	l,a	l,a	l	l	l	l	l	l	l	l	l	0	0	0	0	0	0
	Oeceoptoma noveboracense	0	0	0	0	0	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Staphylinidae	*not identified*	0	0	a	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Creophilus maxillosus	0	0	0	0	0	0	0	0	0	0	0	0	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scarabaeidae	*Onthophagus sp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a

B

Days Postmortem		0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52	54
Family	**Genus and Species**	Fresh		Bloat				Active																					
Calliphoridae	*Cochliomyia macellaria*	a	a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l,a	l	l	l	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p	l,p
	Lucilia coeruleiviridis	0	a	0	a	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Protophormia terraenovae	0	0	0	0	0	0	l	l	l	l	l	l	l	l	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Lucilia illustris	0	a	l,a	l,a	l,a	l,a	l,a	l	l	l	l	l	l	l	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piophilidae	*Piophila casei*	0	0	0	0	0	0	0	a	a	a	a	a	a	a	a	a	a	a	a	0	0	0	0	0	0	0	0	0
Silphidae	*Heterosilpha ramosa*	0	0	0	a	a	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Oeceoptoma noveboracense	0	0	0	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Staphylinidae	*Creophilus maxillosus*	0	0	0	0	0	0	0	0	0	0	0	0	a	a	a	a	0	0	0	0	0	0	0	0	0	0	0	0
Scarabaeidae	*Onthophagus sp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a

Light shading indicates very low and/or inconsistent numbers of individuals collected across all three carcasses. Dark shading indicates consistent and predictable occurrence of individuals. Abbreviations: a = adults, p = pupae, l = larvae, e = eggs.

At the beginning of the active decay stage, core maggot mass temperatures ranged from 35 °C to 36 °C in both habitats. Oddly, these high temperatures were not reflected in the internal temperature readings from the sun-exposed carcasses. From day 19 to 23, core temperatures decreased, ranging from 23 °C. Pupae were first observed on the one shaded carcass without extensive scavenging on day 19. Attempts at rearing the pupae were unsuccessful. However, larval rearing from collections on day 19 resulted in the emergence of two species of blow flies: *L. illustris* and *C. macellaria*. It is possible that pupae had entered diapause due to the shortened day length and low temperatures.

At the sun-exposed sites, pupae were first collected on day 21. Rearing attempts were also unsuccessful. Larval rearing from collections resulted in the emergence of *P. regina* and *C. macellaria*. After day 19, insect activity decreased dramatically. Adult blow flies were rarely seen after day 21. Several muscid flies were collected from the sun-exposed site during active decay, including *Hydrotaea* and *Morellia* (Table 7). Adult *P. casei* were collected on day 11 and day 13 at the sun-exposed and shaded sites, respectively. Although immature specimens were never collected, they may have been developing deep inside the carcass. The cheese skipper remained a dominant insect in both habitats until day 37 and was not collected past day 39.

Immature Silphidae were occasionally collected from sun-exposed sites starting from day 26, but were never recovered from shaded sites. The lack of larval representation of Silphidae at the shaded sites may be a result of the extensive perturbation by badgers. The Scarabaeidae, represented by a single genus in both habitats, were first collected on day 26. The scarab beetles were typically hovering over the carcass or feeding in groups inside the carrion tissues. Throughout October, they were the most common beetles at sun-exposed carrion. They were also common at shaded carrion but were observed in much lower numbers. By the end of the experiment, the only insects at shaded carrion were developing *C. macellaria* larvae. The sun-exposed carrion had the addition of *Onthophagus* Latreille, which remained abundant even on the last day of collection.

4. Discussion

We theorized that the carrion fauna in the grassland ecoregion of Saskatchewan would be unique compared to other geographical regions. Many of the specific species collected in this study have not been reported on carrion elsewhere. However, specific families of insects associated with carrion and their time of arrival are comparable to studies in other regions. For example, Rodriguez and Bass [2] reported the arrival of silphid adults in the fresh stage. In the present study, carrion beetles were the first coleopterans to arrive on all carcasses, regardless of season or habitat. Rodriguez and Bass [2] also report immature silphids arriving in the decay stage and remaining abundant into the dry stage. This pattern was also evident in Saskatchewan with immature carrion beetles characteristic of active decay, advanced decay and dry stages of decomposition. Larval silphids were never collected before active decay in any season or habitat. Interestingly, several researchers [1,5,3] do not report the presence of any immature carrion beetles on carrion.

4.1. Variable habitat

Until recently, previous research on the effect of habitat has been sparse. De Souza and Linhares [31] examined two small pig carcasses in both shade and sunlight over four seasons. However, they did not make observations on decomposition and were mainly concerned with the comparative analysis of the seasonal abundance of blow flies. Furthermore, they did not report the differential insect patterns associated with sunlit and shaded habitats. Shean et al. [11] specifically examined the effect of direct sunlight versus shade on carrion decomposition and insect colonization. However, they examined only one carcass in each habitat, creating the potential for anomalous results. Several Canadian studies have examined multiple pig carrion in variable locations, habitats and seasons [5,17,32–35]. Replicate pigs were also utilized in the present study to avoid anomalous observations across the variables of season and habitat.

Comparable to the findings of Shean et al. [11] and Dillon and Anderson [32], shaded site temperatures were typically higher in the evenings and fluctuated less than sun-exposed sites in all seasons. However, only in the spring season did the ambient temperatures between sun-exposed and shaded habitats differ significantly ($p = 0.01$). This contributed to the greater differences in the decay rate between sun-exposed and shaded carrion in the spring season. Shean et al. [11] concluded that ambient air temperature was a chief factor influencing carrion decomposition. These findings are confirmed by the present study, as the decay rate of sun-exposed carrion differentiated from shaded carrion only in spring when the ambient temperature was significantly different between the two habitats (Table 8).

Enormous variation was observed in the seasonal difference of the internal carcass temperatures of both habitats. In spring, sun-exposed carrion had a 7.8 °C higher average internal temperature than the shaded carrion (Fig. 1). In contrast, shaded pigs in summer experienced higher internal temperatures, averaging a 3.9 °C increase over sun-exposed carrion (Fig. 3). Unfortunately, the internal carcass temperatures of shaded carrion in the fall season were lost, preventing comparison. Summer carrion progressed through the stages of decay at the same rate, even though shaded carrion had significantly higher internal temperature readings. Thus, internal carcass temperature is not highly related to the rate of decay. However, internal temperatures are elevated by larval heat generation and are an important factor for the development rate of larvae.

Several authors have confirmed that internal temperatures of carrion are elevated over ambient during decomposition due to bacterial metabolic reactions [1,2,5,11]. The movement and metabolic activity of maggots, when formed in masses, also generates thermal energy and contributes to the overall elevation of internal temperatures [36,37]. In the present study,

Table 8
Comparison of decay rates in various seasons and habitats in different regions in Canada

Season, Province [reference]	Days postmortem									
	Fresh		Bloated		Active Decay		Advanced Decay		Dry/Remains	
	Sun	Shade	Sun	Shade	Sun	Shade	Sun	Shade	Sun	Shade
Spring, SK	0-1	0-2	2-12	3-15	13-30	16-35	31-42	36-45	42- 63+	46-63+
Spring, MB [35]	0-7	0-9	7-12	9-13	12-17	13-23	17+	23+	n/a	n/a
Summer, SK	0	0	1-4	1-4	5-11	5-11	12-25	12-25	26+	26+
Summer, MB [35]	0-2	0-2	2-6	2-8	6-10	8-13	10+	13+	n/a	n/a
Summer, BC [5]	0-1	_	2-10	_	11-16	_	17-42	_	43+	_
Summer, AB [17]*	0-1	0-2	2-10	3-14	11-16	15-25	17-25	26+	26+	n/a
Fall, SK	0-2	0-3	3-11	4-11	12+	12+	n/a	n/a	n/a	n/a
Fall, MB[35]	0-3	0-3	3-9	3-9	9-12	9-14	12+	14+	n/a	n/a

*Averaged numbers from several pigs in the mid-size range (36–80 kg).

maximum internal temperatures without daily fluctuations always coincided with the presence of 3rd instar blow fly larvae. Subsequent drops in internal temperatures coincided with the migration of post-feeding larvae. However, the presence of 3rd instar larvae did not always result in maximum temperatures for extended periods. Regardless of habitat, the initial peaks in internal temperature always occurred during the active decay stage of decomposition. These observations confirm the findings of Early and Goff [3] and Anderson and VanLaerhoven [5].

The level of heat generation is specific to each habitat. Large maggot masses were observed on shaded carrion in spring in the beginning of active decay. However, internal temperatures reached a maximum of only 6 °C over ambient from the bloated stage until the first pupae were recovered. During this period the ambient temperature was often higher than the internal temperature, also reaching a maximum of 6 °C over internal. In contrast, the internal carcass temperature of sun-exposed carrion during this same period reached as high as 23 °C over ambient. These observations confirm the findings of Dillon and Anderson [32] and Turner and Howard [37], who also noted inconsistencies in the level of elevation of internal temperatures over ambient in different habitats.

There are few generalizations that can be made on the effect of shade or sunlight on decomposition in the Prairie Ecozone. Discrepancy in the rate of decay was only observed in spring and in the first two stages of decomposition in fall. Summer carrion decomposed at the same rate regardless of habitat. These findings are contrary to Shean et al. [11] and Gill [35], who reported differential decomposition between shaded and sunlit pig carcasses in summer. Both of these studies initiated 2–3 weeks prior to the calendar start date of the present study and may account for the differential results.

Shaded carrion in spring and summer retained more abdominal skin and moisture than sun-exposed carrion. In summer, when the ambient temperatures were similar, these differences did not affect the rate of decay. Otherwise, there were no major differences in the pattern of decomposition. Regardless of season, carrion in both habitats exhibited the same gross morphological changes, albeit at different rates in spring and fall.

Habitat variations affected species diversity. Sun-exposed carrion attracted a greater diversity of species and a greater number of each species, compared to shaded carcasses in spring and fall. Similar patterns were reported by Hobischak et al. [33] in spring in Alberta. In spring, a total of 37 forensically significant species were collected from both habitats (Tables 2 and 3). Of the 37, 21 of the species were common to both sun-exposed and shaded habitats. The blow fly *C. vicina* was exclusive to sun-exposed carrion in spring, whereas *L. silvarum* was exclusive to shaded carrion. Both habitats were colonized by the scarab beetle *Aphodius* sp., although the sun-exposed carrion also attracted *Phanaeus* sp.

In summer, insect diversity was reduced in both habitats. A total of 21 species were collected, 8 of which were common to both habitats (Table 5A and B). Shaded carrion attracted a greater diversity of insects in the advanced decay and dry/remains stage. This is likely a reflection of the higher levels of moisture that were retained on these carcasses. Both *C. maxillosus* and *Lobrathium* sp. were exclusive to shaded carrion. The blow fly *P. regina* was present in all three seasons, but was not a common visitor on shaded carrion in summer and fall. The maximum threshold for *P. regina*, 45 °C is relatively

high compared to other species of blow flies [37]. Thus, *P. regina* would have a competitive advantage over other species at sun-exposed carrion during periods of high temperatures. However, most species demonstrated longer periods of colonization on shaded carrion. Interestingly, this was not a factor of a slower rate of decay, but of the potential of the carcass to remain an appropriate resource for insects.

In the fall, a total of 21 forensically significant species were collected, although only 6 of these species were common to both habitats (Table 7A and B). Sun-exposed carrion had the greatest diversity of Calliphoridae colonizing the remains. However, several of these species were rare visitors, including *L. sericata*, *C. vomitoria*, and *C. vicina*. The occasional visitation by these species is likely due to the seasonal changes, cueing several species for diapause. The majority of coleopteran species were identical in both habitats.

4.2. Differences in season

Several previous studies have been conducted in only one season, usually in summer [1,3–5,11,17] with some notable exceptions [2,7,15,17,32–35]. Table 8 compares the decay rates in Saskatchewan with other Canadian studies [5,17,35]. The Manitoba [35] and Alberta [17] experiments are excellent for comparison as both studies: utilized pigs in the mid-size range (36–80 kg); have similar climates; and are relatively close geographically to Saskatchewan, albeit in different ecozones. Decomposition of carrion in Manitoba [35] in spring is similar to Saskatchewan, although the duration of the fresh stage is considerably longer and the active decay stage is shorter (Table 8). These differences are likely due to calendar differences in the start of the experiments. The long duration of the fresh stage in spring in Manitoba may also be due to the predefined stages of decomposition outlined by the researcher.

The rate of decomposition in summer in Saskatchewan was most similar to Manitoba. Although the early stages of decay are accelerated in Saskatchewan, the Manitoba and Alberta experiments had earlier start dates, likely exposing carrion to much cooler temperatures at the start of the experiment. In comparison with the summer decay rates of Anderson and VanLaerhoven [5] in British Columbia, decomposition occurred at a faster rate in Saskatchewan (Table 8). Anderson and VanLaerhoven [5] noted that rainfall impacted insect activity and delayed the onset of decompositional stages. Additionally, the climate in Saskatchewan in summer is warmer and more arid than British Colombia and may account for the rapid decomposition and dehydration of carrion. Rates of decay in fall were the slowest of any season and were very similar to reported rates for Manitoba [35].

In spring and summer, decomposition closely followed the stages outlined by Anderson and VanLaerhoven [5]. The final stage of decay was a combination of semi-skeletonization combined with the mummification of remaining tissues. Interestingly, Anderson et al. [34] also report mummification in Alberta, another region with an arid climate. In fall, sub-zero temperatures in October prevented further decay. Thus, decomposition progressed through only three stages before the experiment ended.

Several authors [1,2,3,5] delineate the end of the bloated stage by the deflation of the carcass when larval feeding breaks the skin. The process is described as if deflation were instantaneous upon rupturing of the tissues. In Saskatchewan, regardless of season or habitat, deflation was a slow process. Deflation took place over a 4-day period in summer, a 12–15 day period in spring, and a 10–11 day period in fall. Reed [38] and Anderson et al. [34] mark the end of the bloated stage and beginning of the active decay stage by the complete cessation of bloat in carrion. However, use of this marker would be misleading in Saskatchewan, as the characteristics of active decay are concurrent with slow deflation. Thus, in Saskatchewan, the end of the bloated stage and initiation of the active decay stage are best defined by the following combination of characteristics: presence of liquefaction and associated froth, the burst of maggots outside of body cavities, and the initiation of deflation. The differential characteristics used to mark the end of the bloated stage in this experiment may account for the differences in the duration of the bloated stage in comparison to experiments in other regions of Canada (Table 8).

The carrion fauna was notably impacted by season. The greatest diversity of dipteran species occurred in spring and fall. This is contrary to the findings of Tabor et al. [7], who noted decreased dipteran diversity in fall. The immediate arrival of blow flies agrees with the findings of other studies [1,2,5,11], however, the specific species varied by season. In spring, *C. cadaverina*, *P. regina*, and *P. terraenovae* arrived first, whereas *C. macellaria* was the first colonizer in summer and fall. However, *P. regina* was still a relatively early colonizer in summer, similar to the patterns noted in Manitoba [35], British Colombia [5] and southwest Virginia [7]. The presence of *P. regina* slightly later in fall agrees with the findings of Gill [35] and Goddard and Lago [39]. In spring, *P. terraenovae* was a pioneer species in both habitats, similar to the experiments in Alberta [33,34]. The very late arrival of *C. macellaria* in spring (day 43) was likely due to the seasonal abundance of this more southern latitude-inhabiting blow fly [19]. The presence of *C. macellaria* is a novel finding, as this species has not been previously reported in Canada east of Ontario. It is likely that the northern range of this species is being expanded, which may impact insect succession of early colonizers in Canada. The presence of *L. silvarum* is interesting, as this species is a facultative parasite of toads [40]. However, given the biology of this species and sporadic visitation to the carcasses, it is unlikely to have directly colonized the remains.

The house fly *M. domestica* colonized carrion in summer only, corresponding with their peak activity in July and August [41]. Unlike other studies [2,3,5,7,11], members of Sarcophagidae were not overly common in Saskatchewan. Three different species were collected in various seasons, although their abundance relative to other dipterans was low. Furthermore, they were often collected in the vicinity of, but rarely on the carcasses proper.

Analagous to research in other Canadian localities [5,31,35], members of Piophilidae were relatively early arrivers, typically

colonizing remains in the bloated or active stages of decay. Similar to the reports of Early and Goff [3] and Rodriguez and Bass [2], the Cleridae did not arrive on carrion until the dry/remains stage. Oddly, members of the family Dermestidae were nearly absent from the collections. This may suggest that the observational periods were too short to observe their arrival, as *Dermestes* was typically not collected until 200 or more days postmortem in Manitoba [35].

Larval Staphylinidae were collected much earlier than most other studies [1,2,3,5,11]. For example, staphylinid larvae were not collected until 78 days postmortem in summer in British Colombia [5]. Larval staphylinids were collected as early as 16 days postmortem in summer in Saskatchewan, similar to the findings of Hobischak et al. [33]. The arrival of the Histeridae in bloat in spring coincides with the findings of Rodriguez and Bass [2]. However, in summer, the Histerids did not arrive until the dry/remains stage. These findings correspond with the summer decay study of Anderson and VanLaerhoven [5] and Early and Goff [3]. Members of the family Scarabaeidae were frequent colonizers of carrion in active decay in spring and fall. Rodriguez and Bass [2] reported a later colonization for scarab beetles, with peak abundance in the dry stage. Species of Scarabaeidae may be good indicators of active decay in spring and fall, when groups of 5 or more are present on a carcass at a given time. Scarab beetles were absent from the summer collections, similar to the findings of several authors [1,3,5]. Nitidulid beetles were relatively uncommon in the collections and had intermittent periods of colonization in various stages. This is contrary to the findings of some authors [2,5], who note a continual succession and increase in abundance of Nitidulidae from the bloated stage onward. However, Gill [35] notes intermittent colonization for some species of Nitidulidae.

5. Conclusions

This investigation demonstrated that the patterns of decomposition and insect succession varied across different habitats and seasons. Ambient temperature was a critical factor in the determination of the rate of decay in various seasons. Furthermore, the seasonal distribution of insects significantly impacted the species that were recovered from carrion in different times of the year.

Generally, rates of decomposition varied across seasons, while patterns of insect succession varied across season and habitat. However, the effect of habitat on decomposition was considerable in spring. Sun-exposed carrion in spring decomposed at a faster rate and had shorter periods of insect colonization than shaded carrion. Habitat was not a significant factor in the decompositional rate of carrion in summer and fall. Within each season, sun-exposed and shaded carrion exhibited the same morphological patterns of decomposition.

Several families of insects arrived in a predictable sequence, although the pattern varied in different times of the year and in different habitats. Forensically useful indicator species were often exclusive to either the shaded or sun-exposed habitat. Members of Piophilidae arrived early in decomposition, in late bloat or early active decay. Larval silphids were indicative of later stages of decay, as they were never active collected before active decay in any season or habitat. Larval staphylinids were typical of advanced decay or beyond. Other coleopteran taxa, such as members of the Scarabaeidae, Nitidulidae, Histeridae, and Cleridae dominated in later stages of decay, although their presence and colonization times varied across season and habitat.

Further research is needed on the biological and ecological characteristics of the particular species associated with carrion in the Prairie Ecozone. The development rates of northern strains of Calliphoridae needs to be investigated, as insects inhabiting the Prairie region may be more acclimatized to severe daily fluctuations in ambient temperature. Additionally, longer succession studies that continue over winter would be a useful addition to this research. However, the data generated from this research are now available for homicide investigations in Saskatchewan and similar biogeoclimatic regions.

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