Initial Study of Arthropod Succession on Pig Carrion in a Central European Urban Habitat

M. GRASSBERGER[1, 2] AND C. FRANK[2, 3]

J. Med. Entomol. 41(3): 511–523 (2004)

ABSTRACT We conducted a carrion succession study within a restricted urban backyard in the city of Vienna, Austria (16° 22′E, 48° 12′N) from May to November 2001 to analyze sequence and composition of the local carrion visiting fauna. Two medium sized clothed domestic pig carcasses (*Sus scrofa* Linnaeus), were used as surrogate human models. In total, 42 arthropod species from the families Calliphoridae, Sarcophagidae, Sepsidae, Piophilidae, Muscidae, Fanniidae, Sphaeroceridae, Phoridae, Drosophilidae, Anthomyiidae, and Lauxaniidae (Diptera), Formicidae, Braconidae, Pteromalidae, and Vespidae (Hymenoptera), Silphidae, Staphylinidae, Histeridae, Cleridae, and Dermestidae (Coleoptera), as well as species from the orders Isopoda and Acari were collected during the decomposition of these carcasses. A significant feature in this study was the high abundance of *Calliphora vomitoria* (L.) and *Chrysomya albiceps* (Wiedemann). In the experiment conducted May to June, larvae and adults of *C. vomitoria* outnumbered all other blow fly species, followed by *Protophormia terraenovae* (Robineau-Desvoidy), *C. vicina* Robineau-Desvoidy, and *Lucilia sericata* (Meigen). *C. vomitoria* is generally considered to be rural in distribution, where it prefers shaded locations. The presence of this species in rural as well as in urban habitats in Austria precludes this species as biogeographic indicator. In the study beginning in August large numbers of female adults of the nonindigenous blow fly *C. albiceps* began oviposition at day 3 after placement of the cadaver. The predatory second and third instars of *C. albiceps* larvae subsequently almost monopolized the cadaver. *C. albiceps* is generally described as tropical and subtropical species. The observed northward expansion of its range beyond southern Europe obviously decreases the value of *C. albiceps* in estimating place of death, in that it is no longer exclusive to southern regions. Our results clearly show, that caution must be used when drawing conclusions from succession data generated in different geographic areas. Moreover, this study demonstrates, that arthropod mediated decomposition of a 44 kg exposed pig carcass in a central European urban habitat can be completed within 3 wk.

KEY WORDS forensic entomology, insect succession, carrion decomposition, postmortem interval, urban habitat, *Chrysomya albiceps*

A DECOMPOSING CARCASS is a temporary, rapidly changing resource, which supports a large, dynamic arthropod community. In addition to ecological interest, carrion decomposition and succession studies have proven important in forensic entomology. When the sequence of insects colonizing carrion is known, an analysis of the arthropod fauna on a carcass can be used to determine time since death in legal investigations (Anderson and VanLaerhoven 1996). In addition if an insect can be found exclusively in a rural or urban habitat, analysis of the carrion associated fauna may help determining whether the remains have been moved from an urban to a rural environment or vice versa (Catts and Haskell 1990, Erzinclioglu 1989). Differences in decomposition of carrion in relation to biogeography and ecology of necrophagous insect communities have been the subject of several field studies in the last decades. Most of these studies have taken place in rural, sometimes tropical areas outside of Europe, using dogs (Reed 1958), guinea pigs (Bornemissza 1957), rabbits (Bourel et al. 1999, De Jong and Chadwick 1999), baby pigs between 1 and 1.4 kg (Payne 1965), gulls (Lord and Burger 1984a), seals (Lord and Burger 1984b), chicken (Arnaldos et al. 2001), and larger pigs (Avila and Goff 1998, Carvalho and Linhares 2001, Anderson and VanLaerhoven 1996, VanLaerhoven and Anderson 1999, Richards and Goff 1997). The only study, involving human corpses was conducted by Rodriguez and Bass (1983) in Tennessee. So far, no study has dealt with succession and decomposition of larger carcasses within cities in temperate regions. The only studies from Europe we are aware of were published by Bourel et al. (1999), studying succession on rabbit carcasses in northern France, Leclercq and Vaerstraeten (1992),

[1] Department of Medical and Forensic Entomology, Institute for Forensic Medicine, University of Vienna, Sensengasse 2, A-1090 Vienna, Austria (e-mail: martin.grassberger@chello.at).
[2] Institute for Anthropology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria.
[3] Institute for Zoology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria.

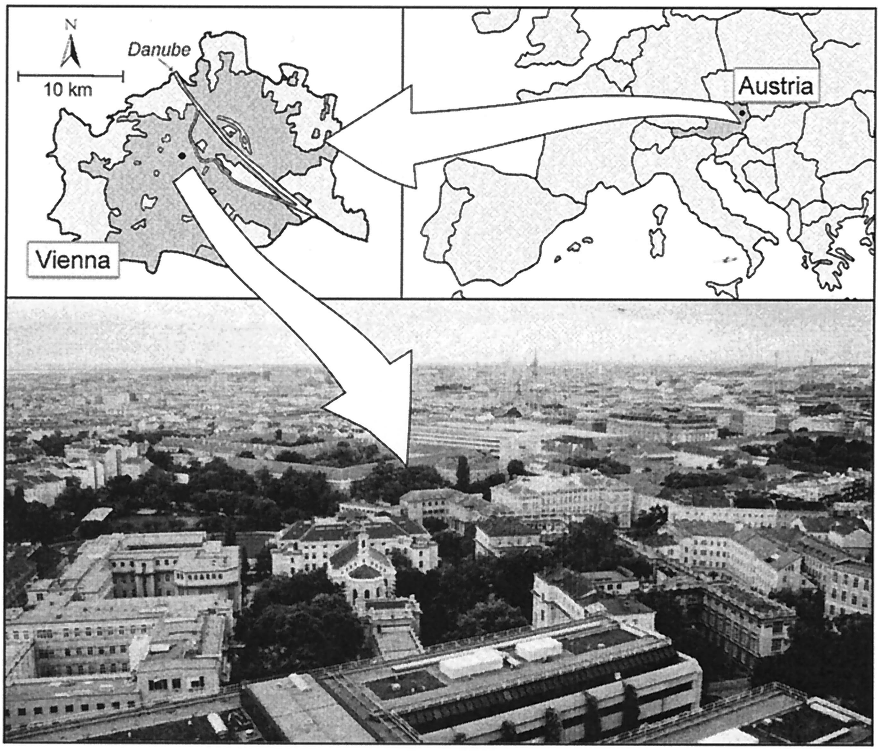

Fig. 1. The study site, a backyard (16° 22′E, 48° 12′ N) within the city of Vienna surrounded by moderate urban vegetation.

using Llama carcasses in grasslands and woods in France and Kentner and Streit (1990), analyzing insect species found at rat carrion.

Because human decomposed cadavers have been repeatedly found in backyards and parks as well as in apartments in the City and in the suburbs of Vienna, we conducted a carrion succession study within a restricted urban backyard from May to November 2001 to analyze sequence and composition of the local carrion visiting fauna. Our principal objective was to evaluate which species may serve as forensic entomology indicators in postmortem interval estimations or proof of corpse displacement in our central European urban setting and which additional influencing factors have to be considered.

Materials and Methods

Carcasses. Two medium sized domestic pig carcasses (*Sus scrofa* Linnaeus), weighing 44 and 37 kg, respectively, were used as surrogate human models, as they are considered to be excellent models for human decomposition (Anderson and VanLaerhoven 1996, Catts and Goff 1992, Rodriguez and Bass 1983). The pig used in the second experiment had a discharging open fracture on the left hind leg. To rule out the risk of disease transmission, a veterinarian examined both pigs before the experiments. The pigs were killed with single shots to the heads from a pin gun. Within 1 h of death, the carcasses were transported to the secure research site on 2 May 2001 (12:00) and 20 August 2001 (22:00), respectively, to study the process of carrion colonization during spring and late summer. The pigs were weighed and clothed with jeans and a white T-shirt. To prevent scavenging by rats and other small vertebrates the carcasses were covered with poultry wire, staked to the ground.

Site Description. Vienna is the capital of Austria with a population of ≈1.6 million, covering 414.95 km^2 (202.64 km^2 green space, 136.07 km^2 built-up area, 56.9 km^2 roads/streets, 19.32 km^2 bodies of water). Its geographical position ranges from longitude 16°11′03″ to 16°34′43″ east and from latitude 48°07′06″ to 48°19′23″ north (Bureau of Statistics City of Vienna).

The study area was located in a secure backyard (16° 22′E, 48° 12′N) some 1.8 km W from the city center (Fig. 1). Elevation of the study site was 175 m above sea level. Coordinates and elevation of the study site were taken on the day of placement with a handheld GPS unit (e-trex vista, Garmin Corp., Olathe, KS).

Predominant vegetation at the experimental site and in the surrounding green was composed of robinia (*Robinia pseudoacacia* L.), ash-tree (*Fraxinus excelsior* L.), aspen (*Populus tremula* L.), yew (*Taxus baccata* L), maple (*Acer sp.*), black alder (*Alnus glutinosa* L.), and chestnut (*Aesculus hippocastanum* L.). The bushes consisted mainly of dogrose (*Rosa canina* L.), elder (*Sambucus nigra* L.), and rowan (*Sorbus aucuparia* L.)

with thick underbrush. Only the immediate site was located in a small clearing with overhead canopy sparse. Adjacent brick walls were heavily grown with ivy (*Hedera sp.*).

These features make this habitat a typical location for homicides or the disposal of human remains within the city. However, it has to be noted, that Vienna is one of the safest cities in Europe with ≈50 homicide cases per year.

On-Site Procedure. Ambient air temperature, relative humidity and precipitation were recorded hourly throughout the whole experiment using a small radio controlled weather station (Conrad Electronic, Germany) placed within 3 m of the carcasses. A two channel NTC-digital thermometer with data logger (MD 3150, Beckmann + Egle, Germany) recorded internal carcass temperature with a probe inserted ≈20 cm into a wound in the thorax created with a scalpel and soil temperature using a 1-h interval. For comparison with data from the experimental site, daily weather data (high, low, mean) were acquired from the Central Institute of Meteorology and Geodynamics (ZAMG), some 3.2 km NW from the study site (16°21′18″E, 48°14′52″N, elevation 190 m). We used Microsoft Excel X for Mac to calculate the linear regression equations predicting on-site ambient temperature from weather data obtained from the weather station.

Both carcasses were visited at least once per day, although during the early stages of decomposition the study site was visited more frequently to record the early processes of insect colonization. The observation period for each experiment lasted for 2 mo. The carcasses were weighed once per week with spring scales. Before examining the carcass, photographs were taken with a Canon EOS-30 using ISO 200 film during each visit.

Adult flies flying around the carcasses were caught with a hand net and transferred to a killing jar containing ethyl acetate. Larvae, when present were collected from each body cavity. When the carcass was weighed, specimens were sampled from the litter under the carcass and on the underside of the carcass itself. Part of the larvae were collected alive from each carcass and were reared to adulthood on beef liver in the laboratory for identification. Another part was killed immediately with hot water and transferred to vials containing 70% ethyl alcohol. In the laboratory all collected adult insects were pinned. Only small numbers of representatives of every life stage of each species were collected to minimize sampling effects. On each visit, the carcasses were thoroughly examined visually for decompositional changes without being disturbed. Observations were recorded and photographed.

Results

Temperature. In general, temperatures in the months May to August 2001 were ≈1–4°C above the average in Vienna, whereas temperatures in September were up to 3°C lower than expected. There was less fluctuation in soil and internal carcass temperature than in ambient air temperature overall, as illustrated by data presented in Figs. 2 and 3. After *algor mortis* was complete, there was little difference between internal carcass temperature and soil temperature, except when the maggot mass passed the temperature probe located inside the pigs thorax (Fig. 2b). In general weather station ambient air temperature was a good predictor of the local ambient air temperature ($r^2 = 0.94$). Only the mean lower temperature at the research site was on average 1.5–2°C above the mean lows of the nearest weather station ($r^2 = 0.85$) probably because of the insulating effects of the surrounding buildings. On day 5 of the second experiment the datalogger of the thermometer failed and readings of the internal carcass temperature and soil temperature were taken manually once per day.

Decomposition Stages. Though decomposition is a continuing process, for convenience in discussing the results, it can be divided into stages. However, these stages do not necessarily represent the appearance or disappearance of specific species or insect groups, as these are not abrupt changes in the insect fauna (Schoenly and Reid 1987), but rather are recognizable stages in the physical decomposition of the carcasses. We defined four stages of decomposition (fresh, bloated, decay, dry/remains) using the criteria set forth by Reed (1958). The fresh stage began at the moment of death and continued until bloat was evident, with no odor emanating from the carcass. The bloated stage was characterized by color changes as well as onset of marbling and bloating or swelling with bubbles of blood forming at the nostrils. In later part of this stage odor becomes noticeable and fluids seep out. The onset of the decay stage was marked by the complete deflation of the carcass, because of feeding Calliphoridae larvae breaking the skin, and strong putrefaction odor associated with tissue liquefaction. In the dry stage skeletonization is almost complete with bones cartilage and some tissue remaining. There was little odor associated with the remains by this time.

Insect Succession. A total of 42 taxa of arthropods, representing four orders and 22 families were collected during both experiments. Only one species was not an insect: *Porcellio scaber* Latreille (Isopoda: Oniscidae).

Experiment 1 (2 May 2001, 12:00). A few minutes after placement, the first flies observed to frequent the cadaver during the fresh stage (Fig. 6A) were Calliphoridae species of the genus *Calliphora* and *Lucilia,* with *C. vomitoria* (L.) dominating. The first egg patches were observed after 3 h in and around the natural orifices of the head as well as around the gunshot wound. Hatching of the blow fly eggs occurred within 24 h, at which time the emerging larvae began feeding on the fluids seeping from the natural orifices. By noon of the second day, female adults of *Protophormia terraenovae* (Robineau-Desvoidy) and *Phormia regina* (Meigen) began to visit the carcass but no larvae of these species were collected until day 5 and 7, respectively. A few adult Sarcophagidae, Piophilidae and Muscidae were also observed at the ca-

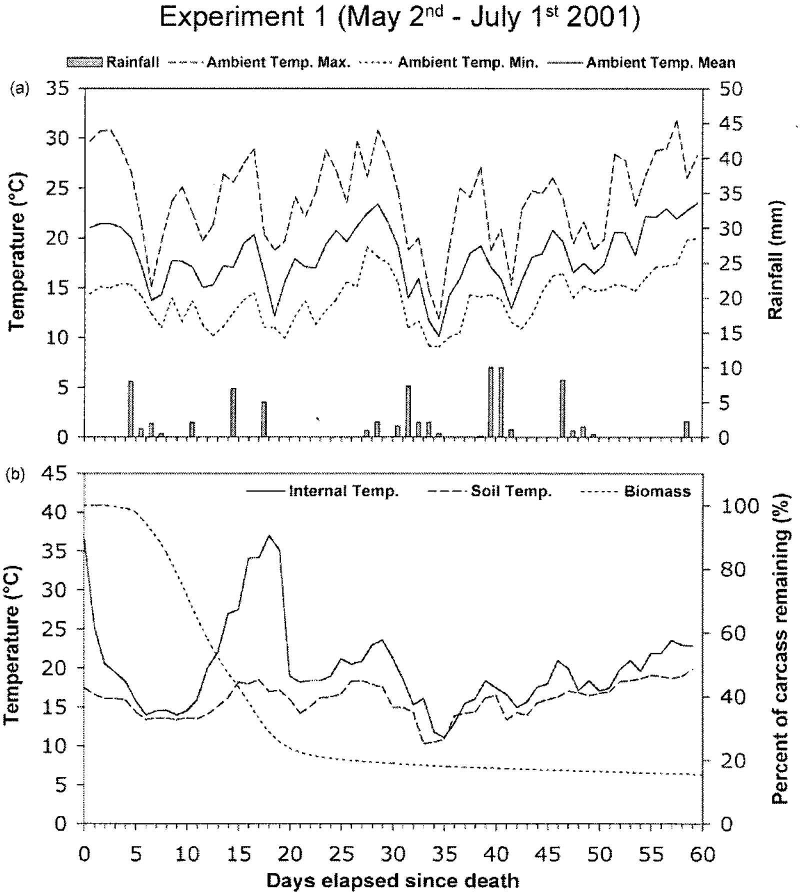

Fig. 2. Maximum, minimum and mean ambient air temperature (°C) and daily rainfall (mm) at the research site during experiment 1 (a). Percent weight loss and mean daily internal carcass and soil temperature during decomposition of pig carcass one (44 kg) placed on 2 May 2001 (b).

daver and the surrounding vegetation. At the end of the second day, the bloated stage began to become visible.

On the morning of the third day the cadaver had a definite bloated appearance. During that stage adults of the dipteran families Calliphoridae, Muscidae, Sarcophagidae, Fanniidae, Phoridae, Drosophilidae, Syrphidae, and Sepsidae were collected from the carcass. Adults of *Calliphora vomitoria, Calliphora vicina* Robineau-Desvoidy, *Protophormia terraenovae, Phormia regina, Lucilia sericata* (Meigen), *Lucilia caesar* (L.), and *Ophyra leucostoma* (Wiedemann) were reared from larvae collected during days 3–10. Among the Hymenoptera, *Alysia manducator* Panzer (Hymenoptera: Braconidae), *Vespula germanica* (F.) (Hymenoptera: Vespidae), and *Lasius niger* Foerster (Hymenoptera: Formicidae) were collected. Ants of the species *Lasius niger* continuously removed eggs and first instar larvae from the cadaver during the first 2 wk of the experiment. Beetles of the families Cleridae and Silphidae were observed regularly from day 5 and 7 on, respectively. From day 7 on the blow flies began to lay large egg masses on the clothing especially on the waistband of the trousers, possibly attracted to areas of body fluid accumulation and seepage. The hatching larvae fed, at least for some days, exclusively on the leaking body fluids. Internal carcass temperature increased considerably as maggot masses developed. The bloated stage lasted up to day 11 with ≈40% of the carcass weight lost at the end of this stage.

The first mass exodus of postfeeding third instars from the carcass occurred at the beginning of the decay stage on days 12–14 consisting of larvae that fed primarily on tissues of the head and the upper thorax aperture (Fig. 6B). On day 16 large masses of feeding second and third instars of calliphoridae larvae from later successional waves gathered at the waist and abdomen (Fig. 6C), subsequently shifting the T-shirt cranially within one day (Fig. 6D). Coleoptera and adult Diptera other than Calliphoridae were collected (Table 1) but the dominant insects by far were larval Calliphoridae. Maximum internal carcass temperature peaked around day 18 when the maggot mass passed the temperature probe inserted in the thorax (Figs. 2b and 6D, E). On days 19 and 20 the last mass exodus of fly larvae occurred (Fig. 6D). By that time the soil

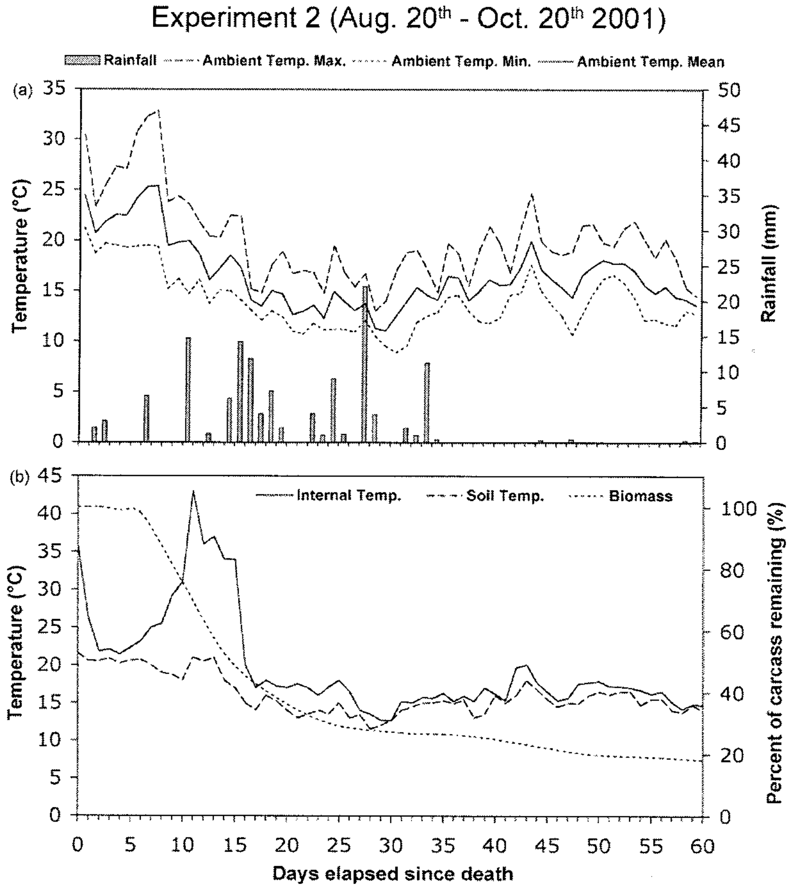

Fig. 3. Maximum, minimum and mean ambient air temperature (°C) and daily rainfall (mm) at the research site during experiment 2 (a). Percent weight loss and mean daily internal carcass and soil temperature during decomposition of pig carcass two (37 kg) placed on 20 August 2001 (b).

surrounding the cadaver contained many fly larvae, which had either pupated or had begun pupation. From day 20 on large numbers of postfeeding third instars of *P. terraenovae* began pupation on the clothing as well as within and under the remains. Three days later parasitoid wasps of the species *Nasonia vitripennis* (Walker) were observed ovipositing on the exposed pupae of *P. terraenovae.* Ants of the genus *Camponotus* were also observed to prey on these pupae, leaving many empty puparial shells. The first adult Dermestidae were collected at day 19 and the first larvae on day 52.

The onset of the dry/remains stage (between day 27–33) was more difficult to define than the previous stages because of the lack of events marking the beginning of the stage (Fig. 6 F). During that stage, a few adult Calliphoridae were still attracted to the remains, but did not lay eggs. Recently emerged teneral adults of *P. terraenovae* were observed on the remains by day 30. Adults and immatures of the genera *Piophila, Ophyra, Muscina,* and *Fannia* were collected, together with adult Sepsidae. Coleoptera of the families Cleridae, Histeridae, Dermestidae (mainly larvae), Staphylinidae (larvae), and Silphidae (larvae) dominated on the carcass, feeding on fly larvae and the remaining tissues. Beginning at day 50, 27 d after the observed oviposition, the first adults of *Nasonia vitripennis* began to emerge in large numbers from the remaining *P. terraenovae* pupae. The carcass was reduced to 16% of its original weight by the end of the observation period (Fig. 2b).

Experiment 2 (20 August 2001, 22:00). From the time of placement no insect activity was noticed until 8:00 the next morning (=day 1) (Fig. 7A). The first fly species observed ovipositing were *C. vicina* and *P. terraenovae.* By noon, ovipositing adults of *C. vicina, Lucilia sp.* and *P. terraenovae* were equally attracted to the suppurating leg wound and to the head of the carcass. At the same time ants began to feed eagerly on the blow fly eggs.

On day 3, when the cadaver was already extremely bloated, large numbers of female adults of *Chrysomya albiceps* (Wiedemann) began to visit the cadaver, resulting in large egg masses around the natural orifices of the head as well as on the leg wound by the end of the day. Adults of *C. albiceps, Calliphora vicina, Lucilia*

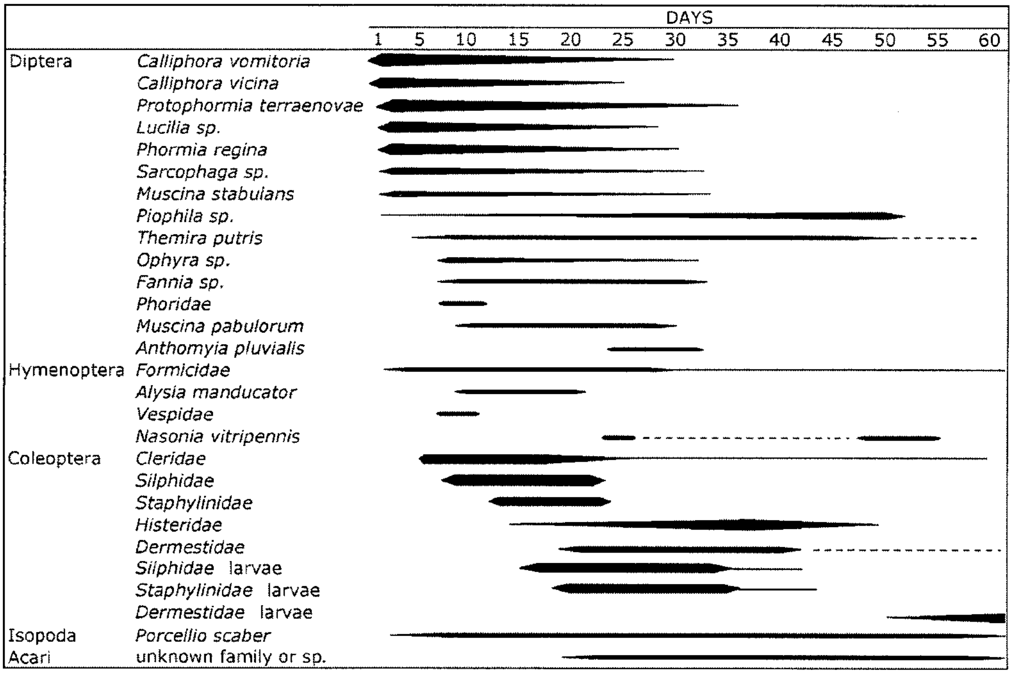

Fig. 4. Chronology of insects at pig cadaver exposed on 2 May 2001 (experiment 1). Thickness of bands indicates relative abundance of each group at different times, based on number of individuals collected and observed during each visit.

sericata, *Ophyra leucostoma*, and *Megaselia scalaris* (Loew) were reared from larvae collected during days 4–10. The first larvae of *C. albiceps* were collected on day 5 and were the predominant species collected and reared from the carcass during this study. Carrion visiting Calliphoridae were often captured by yellow jackets [*Vespula gemanica* (F.), *V. austriaca* (Panzer)], killed and left on the ground surrounding the cadaver. Adult Staphylinidae and Silphidae (Table 1) were observed preying continuously on the larvae of *C. albiceps*, and were collected. Adult Histeridae and Cleridae were also collected. *Alysia manducator* was observed parasitizing third instar larvae of *C. albiceps.* Migrating larvae of *L. sericata* and *C. vicina* were collected on day 9. The bloated stage (Fig. 7B) lasted up to day 10 with ≈30% of the carcass weight lost at the end of this stage.

Ambient temperatures dropped rapidly from day 9 on, but internal carcass temperatures peaked during the following days with temperatures well above 40°C. At day 15 however, internal temperatures fell below 20°C because of heavy rainfalls (Figs. 3a and 7E). No adults of *C. albiceps* were observed at the carcass after day 10, until the first newly emerged teneral adults were collected on days 32/33. The first pupae of *C. albiceps* were collected from the remains and the surrounding soil on day 17. Starting with day 32 the typical egg clusters of *Fannia sp.* were found repeatedly scattered on the remains. The first larvae of *Fannia canicularis* (L.) were collected on day 43. Inside the thoracic cavity and under the remains large aggregations of Silphidae larvae and larvae of *Ophyra leucostoma* were observed and collected. Although adult Piophilidae were present since the beginning of bloating, immature stages were first collected on day 50. The last fly species, attracted to the carcass at day 53 was *Minettia lupulina* (F.) (Dipera: Lauxaniidae). The dry/remains stage was not reached during the observation period (60 d) with ≈20% of the original weight remaining at the end of the study.

Temporal patterns of arthropod succession were determined as described (Figs. 4 and 5, Table 1) and decay curves together with internal carcass and soil temperature were plotted for both experiments, by plotting time (days) against percentage of the carcass remaining (Figs. 2b and 3b).

Discussion

During the interval of 2 May and 20 October 2001 observations of the two cadavers yielded significant information concerning the sequence and composition of the local carrion visiting fauna as well as the duration of decay rates in a central European urban habitat during spring and late summer to autumn. The predominant orders of insects collected during this study were Diptera (25 species) and Coleoptera (10 species). All Diptera were necrophilic taxa with the predominant family of the Calliphoridae (seven species).

Colonization. In the first experiment, large numbers of female Calliphoridae were attracted to the remains within minutes after cadaver placement, with oviposition beginning shortly thereafter. This observation is

Table 1. Succession of insect species collected from two pig carcasses in the City of Vienna during the year 2001

Decomp. stage	Order and family		Genus and species	Sus scrofa 1 2 May–2 July 2001	Sus scrofa 2 20 Aug.–20 Oct. 2001
Fresh	Diptera:	Calliphoridae	*Lucilia sericata* (Meigen)	A	A
			Lucilia caesar (L.)	A	A
			Calliphora vomitoria (L.)	A, E	-
			Calliphora vicina Robineau-Desvoidy	A	A
			Protophormia terraenovae (Robineau-Desvoidy)	A	A
			Phormia regina (Meigen)	A	-
		Sarcophagidae	*Liopygia argyrostoma* (Robineau-Desvoidy)	A	-
			unknown sp.	A	A
		Sepsidae	*Themira putris* (L.)	-	A
		Piophilidae	*Piophila* sp.	A	-
	Hymenoptera:	Formicidae	*Lasius niger* Foerster	-	A
Bloat	Diptera:	Calliphoridae	*Lucilia sericata* (Meigen)	A, L	A, L
			Lucilia caesar (L.)	A, L	-
			Chrysomya albiceps (Wiedemann)	-	A, L
			Calliphora vomitoria (L.)	A, L	-
			Calliphora vicina Robineau-Desvoidy	A, L	A, L
			Protophormia terraenovae (Robineau-Desvoidy)	A, L	A
			Phormia regina (Meigen)	A, L	A
		Sarcophagidae	*Liopygia argyrostoma* (Robineau-Desvoidy)	A, L	A
			unknown sp.	A	-
			unknown sp.	A	-
		Sepsidae	*Themira putris* (L.)	A	A
		Piophilidae	*Piophila* sp.	A	A
		Sphaeroceridae	unknown species	A	-
		Muscidae	*Muscina stabulans* Fallén	A	A
			Muscina pabulorum Fallén	A	-
			Ophyra leucostoma (Wiedemann)	A, L	A, L
		Fanniidae	*Fannia canicularis* (L.)	A	A
			Fannia scalaris (F.)	A	A
		Phoridae	*Megaselia scalaris* (Loew)	A	A, L
		Drosophilidae	*Drosophila funebris* (F.)	A	-
		Syrphidae	unknown sp.	A	-
	Hymenoptera	Formicidae	*Lasius niger* Foerster	A	A
		Braconidae	*Alysia manducator* (Panzer)	A	A
		Vespidae	*Vespula germanica* (F.)	A	A
			Vespula austriaca (Panzer)	-	A
	Coleoptera	Silphidae	*Thanatophilus lapponicus* (Herbst)	A	A
			Thanatophilus sinuatus (F.)	A	A
			Necrodes littoralis (L.)	-	A
		Staphylinidae	*Creophilus maxillosus* (Gravenhorst)	-	A
			Platydracus sp.	-	A
		Histeridae	unknown sp.	-	A
		Cleridae	*Necrobia rufipes* (De Geer)	A	A
			Necrobia violacea (L.)	A	A
	Isopoda	Oniscidae	*Porcellio scaber* (Latreille)	A	A
Decay	Diptera	Calliphoridae	*Lucilia sericata* (Meigen)	A, L, P	A, L, P
			Lucilia caesar (L.)	A, L	-
			Chrysomya albiceps (Wiedemann)	-	A, L, P
			Calliphora vomitoria (L.)	A, L	-
			Calliphora vicina Robineau-Desvoidy	P	A, L, P
			Protophormia terraenovae (Robineau-Desvoidy)	A, L, P	A
			Phormia regina (Meigen)	A, L, P	A
		Sarcophagidae	*Liopygia argyrostoma* (Robineau-Desvoidy)	A, L	-
			unknown sp.	A	A, L
			unknown sp.	A	-

Table 1. (Continued)

Decomp. stage	Order and family		Genus and species	Sus scrofa 1 2 May–2 July 2001	Sus scrofa 2 20 Aug.–20 Oct. 2001
		Sepsidae	*Themira putris* (L.)	A	A
		Piophilidae	*Piophila* sp.	A	A, L
		Muscidae	*Muscina stabulans* Fallén	A, L, P	A
			Muscina pabulorum Fallén	A	-
			Ophyra leucostoma (Wiedemann)	A, L	A, L, P
		Fanniidae	*Fannia canicularis* (L.)	A, L	A, L, E
			Fannia scalaris (F.)	A, L	A, L
			Fannia manicata (Meigen)	-	P
		Phoridae	*Megaselia scalaris* (Loew)	A	A, L
		Drosophilidae	*Drosophila funebris* (F.)	A	-
		Anthomyiidae	*Anthomyia pluvialis* (L.)	A	A
		Lauxaniidae	*Minettia lupulina* (F.)	-	A
	Hymenoptera	Formicidae	*Lasius niger Foerster*	A	A
			Camponotus sp.	A	-
		Pteromalidae	*Nasonia vitripennis* (Walker)	A	-
		Braconidae	*Alysia manducator* (Panzer)	A	A
		Vespidae	*Vespula germanica* (F.)	-	A
			Vespula austriaca (Panzer)	-	A
	Coleoptera	Silphidae	*Thanatophilus lapponicus* (Herbst)	A	A
			Thanatophilus sinuatus (F.)	A	A
			Necrodes littoralis (L.)	A	A
			unknown sp.	L	L
		Staphylinidae	*Creophilus maxillosus* (Gravenhorst)	A	A, L
			Platydracus sp.	A	A
			unknown sp.	L	L
		Histeridae	unknown sp.	A	A
		Cleridae	*Necrobia rufipes* (De Geer)	A	A, L
			Necrobia violacea (L.)	A	-
		Dermestidae	*Dermestes lardarius* L.	A	-
			Dermestes maculatus De Geer	A	-
	Isopoda	Oniscidae	*Porcellio scaber* (Latreille)	A	A
	Acari		unknown sp.	A	A
Dry/Remains	Diptera	Calliphoridae	*Protophormia terraenovae* (Robineau-Desvoidy)	A, P	-
		Piophilidae	*Piophila* sp.	A, L	-
		Sepsidae Anthomyiidae	*Themira putris* (L.)	A	-
	Hymenoptera	Pteromalidae	*Nasonia vitripennis* (Walker)	A, L[a], P[a]	-
		Formicidae	*Camponotus sp.*	A	-
	Coleoptera	Cleridae	*Necrobia rufipes* (De Geer)	A	-
		Dermestidae	*Dermestes lardarius* L.	A, L	-
			Dermestes maculatus De Geer	A	-
		Histeridae	unknown sp.	A	-
	Isopoda	Oniscidae	*Porcellio scaber* (Latreille)	A	-
	Acari		unknown sp.	A	A

A = adults, L = larvae, P = pupae, E = eggs.
[a] Larvae and pupae of *N. vitripennis* recovered from pupal shells of *P. terraenovae.*

in line with other carrion studies (Payne 1965, Anderson and VanLaerhoven 1996) and demonstrates, that there may be no significant delay in colonization of carcasses even in urban habitats. Although Greenberg (1990) reported nocturnal oviposition in a suburb of Chicago at light intensities between 0.2 and 0.7 lux, no oviposition was observed in the second experiment until 09:30 the next morning, rendering the issue of nocturnal oviposition by blow flies a matter of debate.

The described recolonization of both carcasses by calliphoridae species, highlights the importance of collecting the oldest individuals when estimating the postmortem interval based on insect development. The surface debris in the immediate surrounding area should always be removed to expose any migratory larvae or pupae from earlier colonizations.

Ants were collected from both carcasses throughout the decomposition period, feeding on both carrion and insects. In some areas, the removal of eggs by ants, particularly fire ants (*Solenopsis* sp.), can have a major effect on decomposition rates (Greenberg 1991, Payne 1965, Reed 1958), and some authors have found that other species of ant also can have a significant effect on decreasing the decay rates (Cornaby 1974, Lord and Burger 1984a). The ant species found in this study, although present throughout decomposition, did not appear to have a major impact on decomposition rates.

Two to 3 wk after placement of the second cadaver, heavy rainfalls caused the formation of grayish white adipocere (grave wax) within the thoracic cavity and at the abdomen. Its typical malodorous cheesy smell began to attract large numbers of adult *Piophila*, *Fannia*, and *Ophyra* sp. to oviposit. Because areas covered by clothing appear to produce conditions, which favor adipocere formation (Mellen et al. 1993), the use of

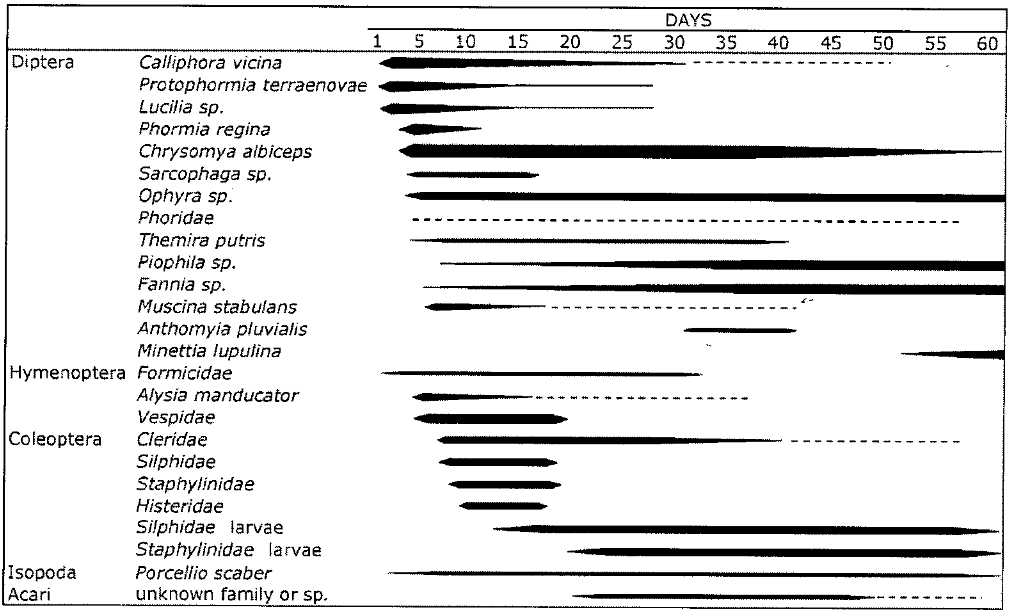

Fig. 5. Chronology of insects at pig cadaver exposed on 20 August 2001 (experiment 2). Thickness of bands indicates relative abundance of each group at different times, based on number of individuals collected and observed during each visit.

dressed carcasses seems to be crucial when investigating the succession of later decay stages for forensic purposes. The absence of adipocere formation during the first experiment prevented by the overall higher temperatures with fever precipitation resulted in dramatically lower numbers of *Piophila, Fannia,* and *Ophyra* sp.

One month after the end of the second experiment a thorough examination of the trouser pockets yielded a number of pupae from which adults of the species *Minettia lupulina* emerged in the laboratory several weeks later. Because dipteran species other than those from the family Calliphoridae could be used as indicator species (e.g., Lauxaniidae), studies on the developmental rates of these species would be important areas of improvement.

Predators/Parasites. Among the Hymenoptera, two parasitic species were observed during the study. Large numbers of the parasitic wasp *Nasonia vitripennis* were found at the cadaver during the first experiment, drilling on the puparia of *P. terraenovae* associated with the remains. Pteromalid wasps, ectoparasitic on fly pupae of various species and worldwide in distribution (Whiting 1967), are commonly used and sold for control of pest flies on feedlots and dairies. Because *N. vitripennis* will only oviposit on fly pupae of a certain age (Whiting 1967) their temperature dependent development can be used to estimate an extended postmortem interval. The fact that *N. vitripennis* was only found during the first experiment with mean daily temperatures still below 25°C may indicate a preference for cooler temperatures and possibly will allow some conclusions about the season of death, when pupal cases with the exuviae of *N. vitripennis* are found in association with human remains. *A. manducator,* a braconid wasp parasitic on Calliphoridae larvae and pupae, was observed attacking second and third instar larvae during both experiments, but no adult wasps emerged in the laboratory from the collected specimen. Because pupal parasitoids of blow flies could play a major role in the estimation of the postmortem interval (Leclercq and Tinant-Dubois 1973, Anderson and Cervenka 2002) future studies are desirable to investigate this matter.

Biogeography. In the experiment conducted May to June larvae and adults of *C. vomitoria* outnumbered all other blow fly species, followed by *Protophormia terraenovae, C. vicina,* and *Lucilia sericata. C. vomitoria* is generally considered to be rural in distribution (Anderson 2001, Smith 1986), where it prefers shaded locations, whereas *C. vicina* is described as a primarily urban fly species (Smith 1986). The high abundance of *C. vomitoria* within the city of Vienna during spring may be explained by the large number of parks and green spots with urban vegetation. Another explanation could be the reported preference of *C. vomitoria* for larger carcasses (Davies 1990, Greenberg and Tantawi 1993) and might therefore not be found in traps or on smaller carcasses normally used in succession studies. The presence of this species in rural as well as in urban habitats in Austria precludes this species as biogeographic indicator.

In the experiment from August to October large numbers of female adults of the nonindigenous blow fly *C. albiceps* began oviposition at day 3 after placement of the cadaver. The predatory second and third instars of *C. albiceps* larvae subsequently almost monopolised the cadaver, leaving only the well protected

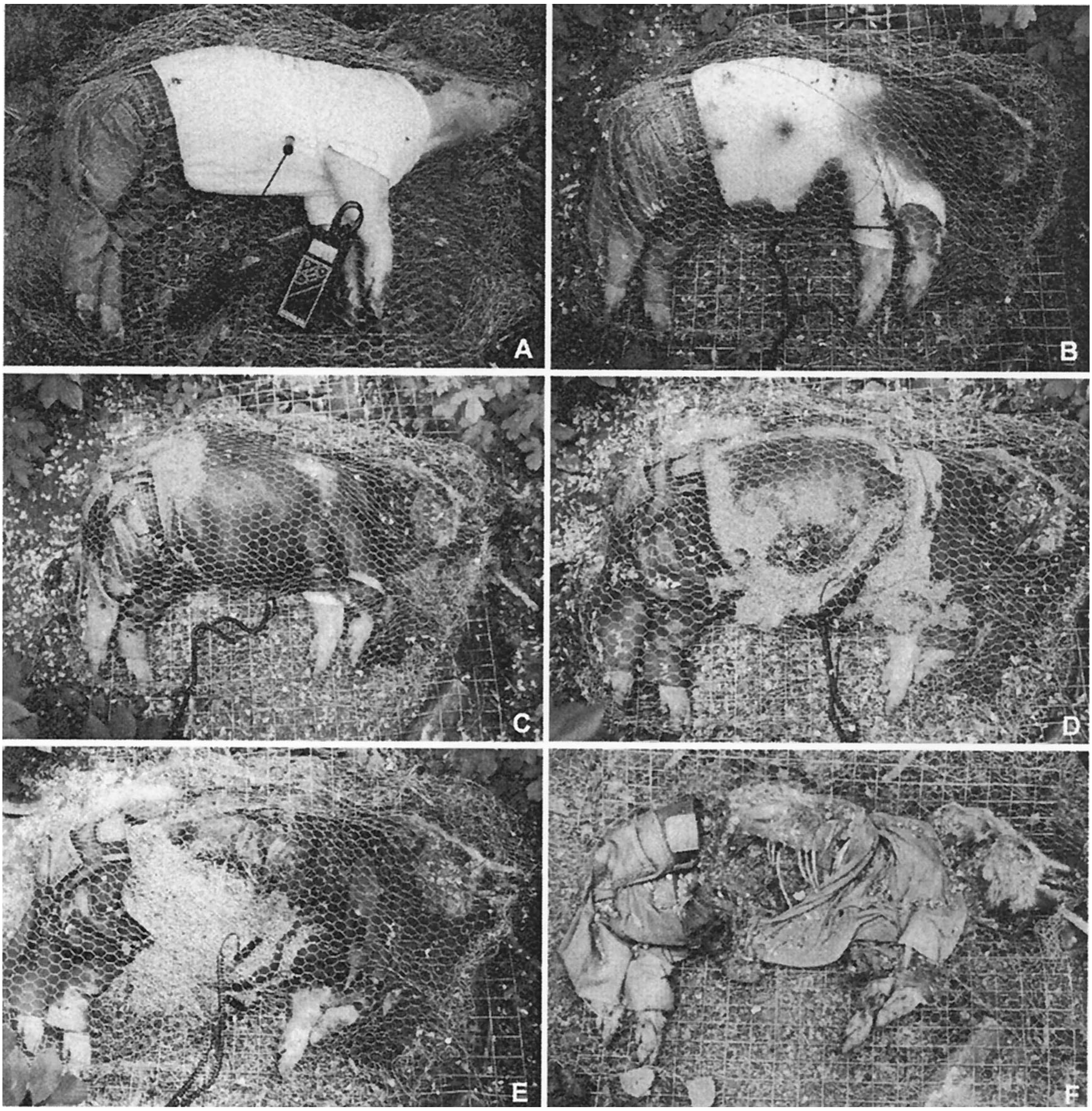

Fig. 6. Decompositional changes during experiment 1 (2 May 2001). (A) Cadaver shortly after placement, fresh stage. (B) day 12, beginning of the decay stage marked by deflation of the carcass. Note that maggot activity is limited to the head and the upper thorax aperture with some larvae feeding on the underside of the body. (C) Day 16. (D) One day later (day 17), the T-shirt was moved cranially owing to insect activity. (E) On day 18, the last aggregation of third instar larvae accumulated in the thoracic/abdominal region. (F) Twenty-seven days after placement of the cadaver, skeletonization was almost complete with patches of mummified skin.

and also predaceous larvae of *O. leucostoma* unharmed. Apart from the current study larvae and pupae of *C. albiceps* were found on several human corpses in and around the city of Vienna during summer 2001 (Grassberger et al. 2003). *C. albiceps* is generally described as a tropical and subtropical species (Hall and Smith 1993). The observed northward expansion of its range, at least during warm summers, beyond southern Europe obviously decreases the value of *C. albiceps* in estimating place of death, in that it is no longer exclusive to southern regions. However, because its abundance seems to be dependent on hot summers and immature development ceases at 15°C (Grassberger et al. 2003), some conclusions about the season of death can be made when pupal cases are found in association with human remains. Moreover, the observed aggressive feeding behavior of second and third instar larvae of *C. albiceps* on local carrion-breeding larvae could reset the postmortem insect clock by clearing a corpse of all earlier arrivers.

Metabolic Heat Generation. Maggotmass temperatures were occasionally raised 25°C above ambient temperature during this study. Previous reports of internal temperatures in carcasses have shown elevated temper-

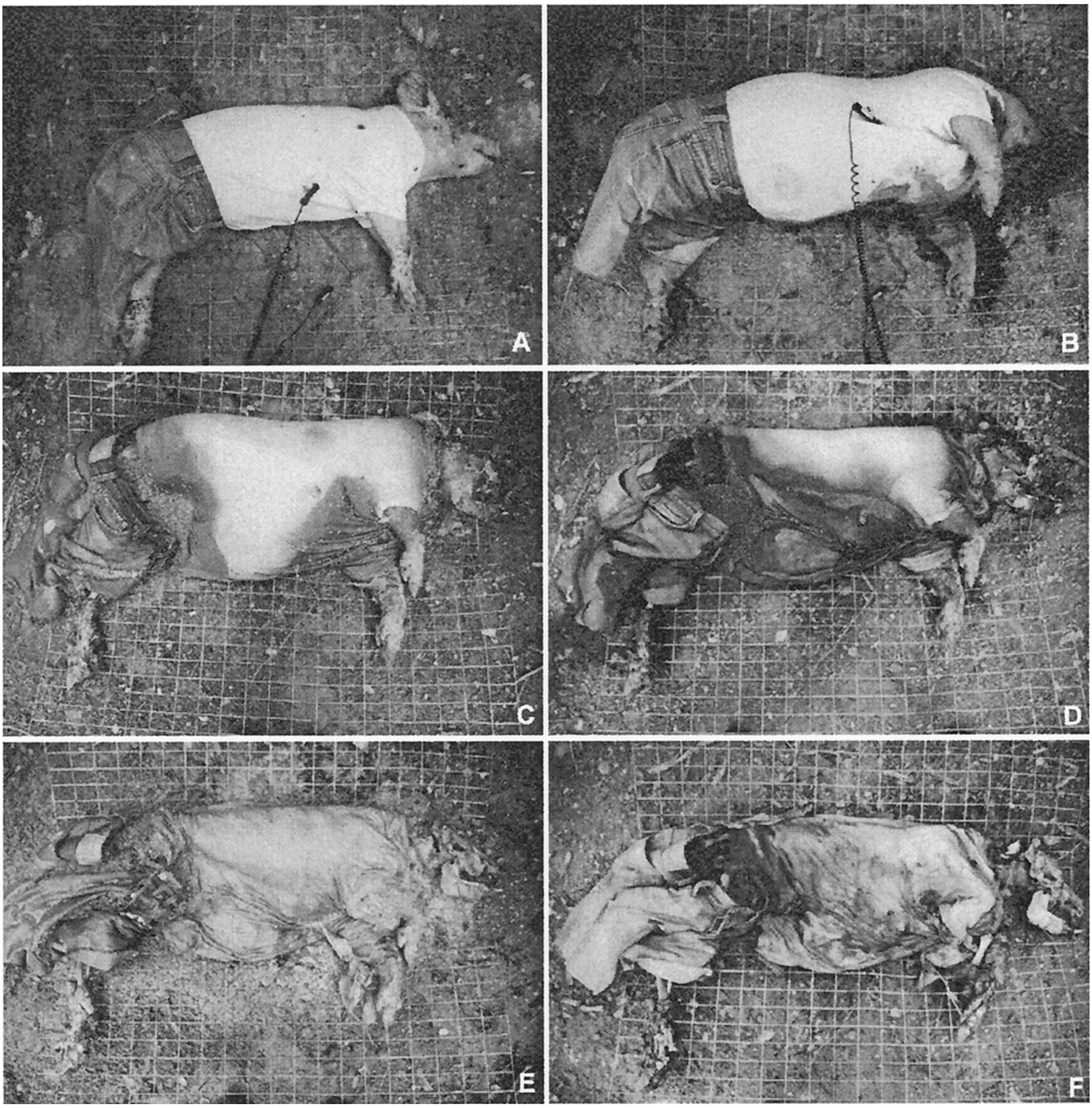

Fig. 7. Decompositional changes during experiment 2 (20 August 2001). (A) Fresh cadaver on the morning after placement with little insect activity. (B) Bloated stage with seeping body fluids 6 d postmortem. (C) On day 11, much of the tissue from the pelvic and abdominal area was removed by feeding third instars of *C. albiceps*. (D) Day 14. (E) Appearance of carcass on day 16 after heavy rainfalls, starting the day before. (F) Although the carcass was mainly skeletonized by day 50, a considerable part of the tissues along the spine and in the thoracic cavity was transformed to adipocere, attracting *Piophila*, *Fannia*, and *Ophyra* sp.

atures (20–40°C above ambient) to be common (Greenberg 1991). Heat generated by dipteran larval aggregations can accelerate larval development within a carcass. Maggotmass temperature peaked earlier in the second experiment, because the temperature probe had to be inserted manually, whereas in the first experiment internal carcass temperature peaked when the maggotmass passed the probe.

Loss of Biomass/Decomposition. Slight variation in the decay rates of the two studied cadavers was observed. In general, weight loss of both carcasses followed a typical S-curve pattern (Figs. 2b and 3b) similar to that of other studies (Anderson and VanLearhoven 1996, Richards and Goff 1997, Payne 1965). However, in the experiment from 20. August, biomass loss was delayed by an interesting sequence of events. The described aggressive colonization of the carcass by the predatory larvae of *C. albiceps* was associated with a drop of the mean daily ambient temperatures below 15°C by 6. September (day 17). Together with the occurrence of heavy rainfalls starting 4 September this led to a reduced internal temperature resulting in retarded larval development in the remaining carcass, and consequently slowed down biomass removal.

The use of larger freshly killed and clothed pig carcasses as surrogate human models in this study resulted in a decompositional pattern similar to that observed in actual forensic cases by the authors. The application of domestic pigs as models for humans in decomposition experiments is well established (Anderson and VanLaerhoven 1996, Avila and Goff 1998, Richards and Goff 1997, Schoenly et al. 1991). They are considered to be the best available model for humans because of their equivalent thoracic cavity size (Schoenly et al. 1991), relatively hairless skin, and omnivorous diet with similar gut fauna (Anderson and VanLaerhoven 1996). In a majority of cases, corpses are completely or partially clothed. Clothes on a cadaver do not delay oviposition, but clothes permeated with lubricants, paint, or combustibles may double the time of initial colonization and retard decomposition by as much as 50% (Marchenko 2001). Conversely, as the clothing gets soiled with blood, urine or fluids leaking in the course of decomposition, it provides more sites for oviposition than a naked corpse, resulting in larger larval masses and, hence, faster decomposition (Anderson 2001). In addition, as the current study shows, egg patches or first instar larvae are not easily washed away by rain, as might be the case with unclothed cadavers (Anderson and VanLaerhoven 1996). Clothing may also slow down postmortem body cooling and favor the onset of the putrefaction process.

One important observation was the ability of the maggot mass to alter the clothing pattern within a very short period of time. These findings are in line with the results of Komar and Beattie (1998), who found that postmortem insect activity frequently reproduces the sexual disarray in clothing patterns seen in cases of sexual assault and sexual homicide.

In the second experiment, ovipositing flies were eagerly attracted to the leg wound, resulting in an accelerated decomposition of the leg and the pelvic area of this pig (Fig. 7C) because of feeding larvae. This supports the notion, that insect activity in areas of normally unbroken human skin, not near a natural orifice, may be an indicator of antemortem trauma (Campobasso and Introna 2001, Haskell et al. 1997)

In a study of postmortem changes in freeze-thawed and fresh killed rats, Micozzi (1986) observed markedly higher rates of external decay and disarticulation in freeze-thawed animals than in freshly killed, untreated controls. We propose that future researchers make it routine practice to use freshly acquired carcasses, instead of frozen carcasses, in their studies of cadaver succession and decomposition. We also suggest the use of clothed carcasses, because clothing can be expected to have an effect on insect succession on a corpse, as it affects the temperature and humidity of the remains, the amount of shade, and protection the body provides.

The biogeography and ecology of necrophagous insect communities are basic to forensic entomology. This study provides valuable information on carrion fauna and their times of colonization of a corps in a central European urban habitat, and shows, that caution must be used when drawing conclusions from data generated in different geographic areas. However, because of the great variability in body decomposition and insect succession, it is imperative that further research be conducted in urban and suburban habitats. Indeed, all aspects of the decomposition and succession process in urban or suburban habitats deserve more attention. There are still many additional habitat types that have not been studied, and the use of entomological techniques for forensic cases in these habitats is still limited. Additionally, as the current study shows, the combination of entomological, pathological, and anthropological indicators in carrion succession studies might open new avenues for discovery of important and little known facts about the pattern of arthropod succession for medicolegal purposes.

Acknowledgments

We express our appreciation to Gerald Takehisa-Silvestri (Department of Anthropology University of Vienna) who provided field support and overall encouragement. We also wish to acknowledge the veterinarian expertise provided by Bernhard Takatsch (Veterinary University of Vienna). This work was carried out by MG in partial fulfillment of his Ph.D. degree at the University of Vienna, Austria.

References Cited

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

Anderson, G. S. 2001. Insect succession on carrion and its relationship to determining time of death, pp. 143–175. *In* J. H. Byrd and J. L. Castner [eds.], Forensic entomology. The utility of arthropods in legal investigations. CRC, Boca Raton, FL.

Anderson, G. S., and V. J. Cervenka. 2002. Insects associated with the body: their use and analyses, pp. 173–200. *In* W. D. Haglund and M. H. Sorg [eds.], Advances in forensic taphonomy. CRC, Boca Raton, FL,

Arnaldos, I., E. Romera, M. D. García, and A. Luna. 2001. An initial study on the succession of sarcosaprophagous Diptera (Insecta) on carrion in the southeastern Iberian peninsula. Int. J. Legal Med. 114: 156–162.

Avila, F. W., and M. L. Goff. 1998. Arthropod succession patterns onto burnt carrion in two contrasting habitats in the Hawaiian Islands. J. Forensic Sci. 43: 581–586.

Bornemissza, G. F. 1957. An analysis of arthropod succession in carrion and the effect of its decomposition on the soil fauna. Aust. J. Zool. 5: 1–12.

Bourel, B., L. Martin-Bouyer, V. Hedouin, J. C. Cailliez, D. Derout, and D. Gosset. 1999. Necrophilous insect succession on rabbit carrion in sand dune habitats in northern France. J. Med. Entomol. 36: 420–425.

Bureau of Statistics of the City of Vienna. 2000. City of Vienna Statistical Yearbook 2000. (http://www.wien.gv.at/english/statistics).

Campobasso, C. P., and F. Introna. 2001. The forensic entomologist in the context of the forensic pathologist's role. Forensic Sci. Int. 120: 132–139.

Carvalho, L.M.L., and A. X. Linhares. 2001. Seasonality of insect succession and pig carcass decomposition in a natural forest area in southeastern Brazil. J. Forensic Sci. 46: 604–608.

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

Catts, E. P., and N. H. Haskell. 1990. Entomology and Death: A procedural guide. Forensic entomology specialties, Clemson, SC.

Cornaby, B. W. 1974. Carrion reduction by animals in contrasting tropical habitats. Biotropica 6: 51–63.

Davies, L. 1990. Species composition and larval habitats of blow fly (Calliphoridae) populations in upland areas in England and Wales. Med. Vet. Entomol. 4: 61–68.

De Jong, G. D., and J. W. Chadwick. 1999. Decomposition and arthropod succession on exposed rabbit carrion during summer at high altitudes in Colorado, USA. J. Med. Entomol. 36: 833–845.

Erzinclioglu, Z. 1989. Entomology and the forensic scientist: how insects can solve crimes. J. Biol. Ed. 23: 300–302.

Grassberger, M., E. Friedrich, and C. Reiter. 2003. The blow fly *Chrysomya albiceps* (Wiedemann) (Diptera: Calliphoridae) as a new forensic indicator in Central Europe. Int. J. Legal Med. 117: 75–81.

Greenberg, B. 1990. Nocturnal oviposition behavior of blow flies (Diptera: Calliphoridae). J. Med. Entomol. 27: 807–810.

Greenberg, B. 1991. Flies as forensic indicators. J. Med. Entomol. 28: 565–577.

Greenberg, B., and T. Tantawi. 1993. Different developmental strategies in two boreal blow flies (Diptera: Calliphoridae). J. Med. Entomol. 30: 481–484.

Hall, M.J.R., and K.G.V. Smith. 1993. Diptera causing myiasis in man, pp. 429–469. *In* R. P. Lane and R. W. Crosskey [eds.], Medical insects and arachnids. Chapman & Hall, London, England.

Haskell, N. H., R. D. Hall, V. J. Cervenka, and M. A. Clark. 1997. On the body: insects' life stage presence and their postmortem artifacts, pp. 415–448. *In* W. D. Haglund and M. H. Sorg [eds.], Forensic taphonomy. The postmortem fate of human remains. CRC, Boca Raton, FL.

Kentner, E., and B. Streit. 1990. Temporal distribution and habitat preference of congeneric insect species found at rat carrion. Pedobiologia 34: 347–359.

Leclerq, M., and C. Verstraeten. 1992. Eboueurs entomologiques benevoles dans les ecosystems terrestres: observation inedited. Note Faun. Gembloux 17–22.

Leclerq, M., and J. Tinant-Dubois. 1973. Entomologie et médicine legale. Observations inedites. Bull. Med. Leg. Tox. Med. 16: 251.

Lord, W. D., and J. F. Burger. 1984a. Arthropods associated with herring gulls (*Larus argentatus*) and great black-backed gulls (*Larus marinus*) carrion on islands in the gulf of Maine. Env. Entomol. 13: 1261–1268.

Lord, W. D., and J. F. Burger. 1984b. Arthropods associated with harbor seal (*Phoca vitulina*) carcasses stranded on islands along the New England coast. Int. J. Entomol. 26: 282–285.

Marchenko, M. I. 2001. Medicoloegal relevance of cadaver entomofauna for the determination of the time of death. Forensic Sci. Int. 120: 89–109.

Mellen, P.F.M., M. A. Lowry, and M. S. Micozzi. 1993. Experimental observations on adipocere formation. J. Forensic Sci. 38: 91–93.

Micozzi, M. S. 1986. Experimental study of postmortem change under field conditions: effects of freezing, thawing, and mechanical injury. J. Forensic Sci. 31: 953–961.

Payne, J. A. 1965. A summer carrion study of the baby pig *Sus scrofa* Linnaeus. Ecology 46: 592–602.

Reed, H. B. 1958. A study of dog carcass communities in Tennessee, with special references to the insects. Am. Midl. Nat. 59: 213–245.

Richards, E. N., and M. L. Goff. 1997. Arthropod succession on exposed carrion in three contrasting tropical habitats on Hawaii Island, Hawaii. J. Med. Entomol. 34: 328–339.

Rodriguez, W. C., and W. M. Bass. 1983. Insect activity and its relationship to decay rates of human cadavers in east Tennessee. J. Forensic Sci. 28: 423–432.

Schoenly, K., and W. Reid. 1987. Dynamics of heterotrophic succession in carrion-arthropod assemblages: discrete series or a continuum of change? Oecologia (Berl.). 73: 191–202.

Schoenly, K., K. Griest, and S. Rhine. 1991. An experimental field protocol for investigating the postmortem interval using multidisciplinary indicators. J. Forensic Sci. 36: 1395–1415.

Smith, K.G.V. 1986. A manual of forensic entomology. British Museum (Natural History), London, and Cornell University Press, Ithaca, NY.

VanLaerhoven, S. L., and G. S. Anderson. 1999. Insect succession on buried carrion in two biogeoclimatic zones of British Columbia. J. Forensic Sci. 44: 31–41.

Whiting, A. R. 1967. The biology of the parasitic wasp *Mormoniella vitripennis* (= *Nasonia brevicornis*) (Walker). Quart. Rev. Biol. 42: 333–406.

Received for publication 1 October 2002; accepted 27 January 2003.