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African Carrion Ecosystems and Their Insect Communities in Relation to Forensic Entomology

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ABSTRACT

African carrion communities contain representatives of the same families that occur in carrion communities on other continents. Checklists and identification guides are tabulated, and the natural histories of core members of the terrestrial community are outlined. Because of strong phylogenetic trends in the biology of the families, the species are effectively ecological surrogates of their relatives elsewhere. These phylogenetic trends also allow the definition of a set of guilds of functionally equivalent species that unify the study of carrion communities world-wide, and a revised suite of guilds is described with both synecological and forensic purposes in mind. Although the decomposition process has been arbitrarily subdivided into stages, they have little direct relation to the dynamics of the carrion community, and should be treated as landmarks rather than phases. Community turnover follows a qualitatively predictable succession, with the greatest species richness and diversity around the ecotone-like transition from 'wet-phase' to 'dry-phase' carrion habitats. These habitats are differentiated along interacting ecological gradients of dietary quality, competition, and risk of predation, which are important to the core guilds. Competition and predation have strong effects on population dynamics of community members, but link particular species only weakly, so that the succession pattern largely reflects the autecology of the individual species. Discrete waves of species are absent, which increases the temporal resolution, and therefore the forensic value, of the succession as a 'clock'. The forensic significance of various aspects of community and trophic dynamics are discussed, and means of applying ecological theory to investigations are reviewed.

Keywords: community composition, community dynamics, ecological succession, guild structure, post-mortem intervals

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INTRODUCTION

Apart from its intrinsic interest, community ecology has value to various branches of applied science including forensic science. The applied significance of carrion insect communities arises from their association with dead vertebrates, including humans. Forensic entomologists use carrion insect communities to produce evidence in cases of murder, suicide, neglect, accident and poaching. These applications have been explored quite extensively in Europe

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Invited Review

(Smith 1986) and North America (Byrd and Castner 2010), but literature about carrion ecology in Africa, Asia, Australia and South America has yet to be consolidated.

African scientists have been aware of the potential of forensic entomology for a few decades (e.g. Blair 1979; Louw and van der Linde 1993; Williams and Villet 2006a), and entomological evidence has been led in trials, at least in South Africa and Zimbabwe (Blair 1979; Gifford 2005a, 2005b; Williams and Villet 2006a). The purpose of this work is to review what is known about carrion-based ecosystems and the insect communities associated with them in Africa, giving attention to the use of this knowledge in forensic entomology internationally. It does not address the full spectrum of forensic entomology, which is very broad, drawing on autecology, developmental physiology and toxicology as well as community ecology, and addressing ecosystems besides carrion (Smith 1986).

The community of insects retrieved from a corpse or carcass is used in forensic investigations primarily to develop an estimate of when the person or animal died, a period commonly termed the post mortem interval (PMI: Smith 1986). It may be more correctly called the Time of Colonisation (TOC: Byrd and Castner 2010) or Period of Insect Activity (PIA: Byrd and Castner 2010) because it is the amount of time that would be required to reach the observed degree of colonization. The body may have been dead for some time before it was colonised (due to many factors including the weather and season), which is why this estimate is treated as a minimum (PMI_{min}) when using developmental biology to estimate it (Villet *et al.* 2010; Villet and Amendt 2011), but when ecological evidence is used, this colonisation period is equivalent to the estimated PMI unless the contingencies of the case cause abnormal delay in colonisation (Villet and Amendt 2011). The information needed to make the ecological estimate includes the identity of the insects (community composition), their role in the community (guild structure), and how the colonisation process progresses (community dynamics). These topics will form the framework of the following discussion.

CARRION AS A FUNCTIONAL ECOSYSTEM

The concept of carrion as a functional ecosystem requires some qualification (Zellmer *et al.* 2006). Carrion is the putrefying flesh of animals, and therefore has relatively consistent chemical, physical and structural characteristics. Carrion is protein-rich, leading to its gradual consumption, fragmentation and dissipation by a variety of organisms, so that it is temporally discrete. It is also spatially discrete (at least soon after death), and often has its own microclimate. Carrion may also attract a predictable, taxonomically distinctive and functionally integrated suite of small-bodied organisms that may be termed the carrion-associated community. A variety of other species may be present less predictably. This community is moderately species-rich, and may contain a few dozen species at any one time. For these organisms, carrion provides a climatically specialised, resource-enriched habitat within the spatial and temporal existence of which they can conduct a significant part of their lives, in particular completing their life cycles. The activities of these organisms lead to broadly predictable processes that affect the carrion over time scales that are longer than the organisms' lifetimes. Carrion therefore presents a tractable ecosystem for ecological experimentation. Conceiving of carrion as a functional ecosystem makes epistemological sense in the context of these smaller organisms. As will be shown, it is also helpful to forensic entomology.

Carrion ecosystems can be broadly divided into two distinct types: terrestrial and aquatic. Carcasses on land usually undergo two physiochemical processes, decomposition and mummification (Smith 1986; Byrd and Castner 2010), while the presence of water leads to saponification of fatty tissue and adipocere formation (Merritt and Wallace 2010); in rare cases they may undergo all three simultaneously (Smith 1986). Buried corpses decay according to the contingencies of how they are buried, and have recently been thoroughly reviewed (Gaudry 2010); they will not be considered further here because of a lack of data from Africa, apart from some notes about the disposal of sheep carrion (Ullyett 1950). The decay processes affect the suite of animals that may be attracted. The functional roles that are played by the mammals and insects that are attracted to terrestrial carrion are dominated by fish and crustaceans in marine and freshwater carrion communities. The vertebrates and crustaceans are opportunistic scavengers with life cycles that are much longer than the transient existence of most carrion. For this reason, when estimating a PMI, they may be excluded from the definition of a carrion community and viewed instead as disturbances (e.g. Richardson 1980; Ellison 1990). Comparable concerns have been raised regarding the forensic significance of aquatic mites (Proctor 2009). In the case of carcasses in fresh or marine water, it is not yet clear whether there are any aquatic organisms that complete their life cycle within carrion (although there are, for example, polychaetes that appear to do so in skeletonised whale bones: Glover *et al.* 2008), which raises the question of whether totally immersed carrion can be said to house a community and whether it is useful to think of it as an ecosystem. Payne and King (1972) did interpret submerged carrion within a community ecological framework. Older studies (e.g. Johnson 1975; McKinnery 1978) used the term 'microcommunity' to recognise that that some of the organisms interacting with carrion were part of a larger-scale 'community' that is not ecologically defined by the carrion. This terminology has been largely abandoned, and it has been recognised that evidence of ecological succession in submerged carrion is scarce (Merritt and Wallace 2010). For these epistemological reasons, and because of the paucity of published data on aquatic carrion in Africa, this review focuses on the functional communities of terrestrial invertebrate carrion. The aerial parts of partially submerged carrion tend to be colonised by the same animals that attend terrestrial carrion, and to have similar community dynamics as a result (Merritt and Wallace 2010).

Carcasses of a number of different vertebrates have been used as models to study carrion communities, one of the most important of which is pig carcasses because they are very similar to human corpses in their size, hairlessness, and subcutaneous adipose layer (Smith 1986); they decompose in a consistent way (Shahid *et al.* 2003; Schoenly *et al.* 2005; Ekanem and Dike 2010) that is similar to human corpses (which enhances their significance to forensic entomology) and attract a statistically comparable insect community (Schoenly *et al.* 2007); they are usually easy and relatively cheap to obtain; and their use does not raise many public objections. However, most of the data for Africa have been gathered from other dead animals (e.g. Meskin 1986), specifically elephants (Coe 1978), antelopes (Braack 1986, 1987; Braack and de Vos 1987; Ellison 1990), rabbits (Tantawi *et al.* 1996, 1998), and fishes and snails (Hegazi *et al.* 1991). Each type of carrion was studied in a different part of Africa, which has probably introduced a geographical bias into the data because there is some partially anecdotal evidence that the size of a carcass influences the composition of the community it attracts (Mönnig and Cilliers 1944; Kneidel 1984; Meskin 1986; Hewadikaram and Goff 1991; Simmons *et al.* 2010). Readers should keep this caveat in mind.

The data are also geographically biased. Carrion studies are heavily focussed on South Africa (reviewed by Williams and Villet 2006a), with a few in Egypt (Hegazi *et al.* 1991; Tantawi *et al.* 1996, 1998) and one each in Kenya (Coe 1978) and Nigeria (Ekanem and Dike 2010). These studies represent urban, desert, grassland, savannah and beach habitats; forest habitats are absent. Apart from differences caused by habitat, the species composition of communities will vary because organisms' geographical distributions will rarely coincide over the spatial scale of a continent the size of Africa, even if they are as mobile as blowflies. This is

Table 1 Checklists of the principal necrophagous African carrion insects.

Taxon	Catalogue	
	Carrion ecosystems	**General**
DIPTERA		
Piophilidae		McAlpine 1977
Muscidae	Tantawi *et al.* 1998 Okiwelu *et al.* 2008 Ekanem and Dike 2010	Couri 2007 Couri *et al.* 2006 (Madagascar) Pont 2009 (Seychelles)
Calliphoridae	Braack 1986, 1987 Hegazi *et al.* 1991 Tantawi *et al.* 1996, 1998 Okiwelu *et al.* 2008 Ekanem and Dike 2010	Zumpt 1956 Kurahashi and Kirk-Spriggs 2006 (Namibia) Verves and Khrokalo 2009a (Seychelles)
Sarcophagidae	Tantawi *et al.* 1998 Ekanem and Dike 2010	Zumpt 1972 Pape 1996 Verves and Khrokalo 2009b (Seychelles)
COLEOPTERA	Prins 1984a, 1984b	
Histeridae	Prins 1984a Ekanem and Dike 2010	Mazur 1997
Silphidae	Prins 1984a	Schawaller 1981, 1987
Staphylinidae	Prins 1984a Braack 1986	
Cleridae	Okiwelu *et al.* 2008	
LEPIDOPTERA	Braack 1986	
HYMENOPTERA		
Formicidae	Braack 1986 Ekanem and Dike 2010	Arnold 1915, 1926
Megachilidae	Okiwelu *et al.* 2008	
ISOPTERA		
Termitidae	Coe 1978 Ekanem and Dike 2010	Uys 2002
SIPHONAPTERA		Segerman 1995
PHTHIRAPTERA		Ledger 1980
DIPLOPODA	Prins 1983 Ekanem and Dike 2010	Hamer 1998

apparently largely due to differences in physiological tolerance to climatic variables like relative humidity and temperature (Richards *et al.* 2009b). To sidestep this problem, this review will focus on the functional aspects of African carrion insect communities and give only brief indications of their precise taxonomic composition. Fortunately, a number of functionally significant carrion insects are widespread (several are synanthropic), so that the examples discussed will have quite wide applicability.

TAXONOMIC COMMUNITY COMPOSITION

Although only a few systematic catalogues of African carrion communities have been compiled (**Table 1**), almost 300 species of arthropods have been recorded. These represent nearly 40 taxonomic families, primarily of insects. These figures are comparable with lists from the Holarctic (Payne 1965; Smith 1986) and the Neotropics (Carvalho and Mello-Patiu 2008; Almeida and Mise 2009).

The uneven level of taxonomic resolution in lists of African carrion insects reflects the attention given to each group as well as their absolute diversity. Continent-wide taxonomic catalogues exist for several important groups (**Table 2**), and many of these contain useful identification keys based on morphological characters of the adults. Keys to immature stages are scarcer but go to species level in blowflies and hide beetles (**Table 2**). Molecular methods of identification have been developed for some groups, allowing the identification of all stages (including eggs) and the linking of immature and adult forms (**Table 2**).

Over 95% of the specimens on a carcass are insects, and a 65 kg impala (*Ampyceros melampus*) carcass can support over 115,000 maggots and 20,600 histerid beetles (Braack 1987). Inventories (**Table 1**) indicate that, while African blowfly populations are numerically dominant, the beetles are more species-rich, and that several other orders of insects may occur predictably or adventitiously. This pattern is also seen on other continents, where members of the same families are often involved, suggesting that ecological principles relating to the African carrion-associated fauna may be applicable in other regions too. This is even more likely because many common carrion insect species are synanthropic and have been spread around the world by human traffic (Prins 1979; Laurence 1988; Braack 1991; Williams and Villet 2006b) and their own dispersal abilities (Povolný 2002; Verves 2004; Rosati and VanLaerhoven 2007).

The diversity and natural history of the most characteristic carrion arthropods are outlined here, along with indication of a few synonyms used in older forensically-relevant literature.

Diptera (true flies)

Blowflies (Calliphoridae) and flesh flies (Sarcophagidae) dominate the decomposition of carrion, but at least 14 other families of flies from across the phylogenetic spectrum may be present. Most families are from the superfamilies Tephritoidea (Han and Ro 2005) and Muscoidea (a paraphyletic group that includes the Oestroidea: Kutty *et al.* 2008), indicating a phylogenetic component to community membership. A dozen of the families occurring in Africa have also been recorded from carrion in South America (Carvalho and Mello-Patiu (2008) and the Holarctic (Smith 1986). Identification of adults can be made using the keys provided by Smith (1986) and Barraclough (1995), and some of the larvae are described by Smith (1986). Fly larvae may be particularly well pre-adapted to living in carrion by their lack of appendages. The most frequently encountered families are discussed here, in phylogenetic sequence.

Table 2 Identification resources for the principal necrophagous African carrion insects.

Taxon	**Morphological identification**		**Molecular identification**
	Larvae	**Adults**	
DIPTERA	Smith 1986	Smith 1986	
		Barraclough 1995	
Phoridae		Beyer 1965	
Piophilidae		McAlpine 1977	
Muscidae	Skidmore 1985	Couri 2007	
	Tantawi and El-Kady 1997	Couri *et al.* 2006 (Madagascar)	
Calliphoridae	Prins 1982	Zumpt 1956	Harvey *et al.* 2003, 2008
	Tantawi and El-Kady 1997		Tourle *et al.* 2008
	Szpila and Villet 2011		
Sarcophagidae	Aspoas 1991	Zumpt 1972	Wells *et al.* 2001
	Tantawi and El-Kady 1997		
COLEOPTERA	Smith 1986	Smith 1986	
Silphidae	Prins 1983	Schawaller 1981, 1987	
Staphylinidae		Newton *et al.* 2001	
Histeridae	Caterino and Vogler 2002	Kovarik and Caterino 2001	
Dermestidae	Rees 1947	Mroczkowski 1968	
	Adams 1980	Peacock 1993	
	Zhantiev and Volkova 1998, 1999		
Ptinidae	Hall and Howe 1953	Brown 1940	
		Irish 1996a, 1996b, 1999	
Scarabaeidae		Scholtz 1987	
		Medina and Scholtz 2005	
		Davis *et al.* 2008	
Trogidae		Scholtz 1980, 1982, 1983	
		van der Merwe and Scholtz 2005	

1. Stratiomyidae (soldier flies)

These flies have a characteristic discal cell in their wing venation. Although over 370 species occur in the region, the Africa soldier flies have not been taxonomically revised. It seems likely that only the cosmopolitan, wasp-mimicking *Hermetia illuscens* has forensic significance in Africa. It breeds in rotting vegetation, including compost heaps, and older carrion and corpses (Lord *et al.* 1994). This species originated in the Neotropics, and no work has been done on its natural history in Africa.

2. Phoridae (scuttle flies)

These are very small, hump-backed flies that can run rapidly. Unidentified specimens of *Conicera*, related to the "coffin fly", *Conicera tibialis*, have been reported from the Democratic Republic of Congo (Beyer 1965), and over 200 species have been assigned to the genus *Megaselia*, which contains known carrion flies (Greenberg and Wells 1998; Disney and Manlove 2005; Disney 2008). Means of identification have not been consolidated. Their natural history is largely unknown, but may be similar to that of the European species (e.g. Colyer 1954; Disney 2005, 2006).

3. Piophilidae (cheese skippers)

Only seven species of Piophilidae are known from Africa, and all breed in carrion (Cogan 1980; Braack 1986). The cosmopolitan species *Piophila casei* is the most likely to be encountered. McAlpine (1977) provided a key to identify adults to species, and then described *Piophila megastigma* from South Africa (McAlpine 1978). Smith (1986) described the natural history of *P. casei*.

4. Muscidae (house flies)

Although over 900 species and 58 genera of Muscidae occur in Africa (Pont 1980; Couri *et al.* 2006; Couri 2007), carrion is regularly visited by very few of them, and it is not clear that any routinely breed in carrion unless excrement is present (Smith 1986). The principal species visiting carcasses are *Musca domestica*, *M. sorbens*, *Muscina stabulans*, *Synthesiomyia nudiseta*, and *Hydrotaea ignava* (= *leucostoma*) (Tantawi *et al.* 1998). These species tend to be cosmopolitan and synanthropic. Keys to the genera exist (**Table 2**), but keys to the species have not been consolidated. Some larvae have been described (**Table 2**). Studies of development of relevant species are scarce and involve non-African populations (Dadour *et al.* 2001). There is a large but scattered literature about the natural history of muscids (Skidmore 1985).

5. Calliphoridae (blow flies)

This moderately diverse family includes about two dozen indigenous species, primarily in the genera *Calliphora*, *Lucilia* (= *Phaenicia*), *Hemipyrelia* and *Chrysomya*, that specialise in breeding in carrion (Zumpt 1965; Prins 1982; Meskin 1986; Rognes and Paterson 2005), as well as some introduced species (Prins 1979; Braack 1991; Williams and Villet 2006b). The morphologically and ecologically distinctive species *Chrysomya albiceps* and *C. rufifacies* have been placed in the genus *Achoetandrus* by some authors, but this renders the genus *Chrysomya* paraphyletic (Harvey *et al.* 2008), and is therefore generally rejected. For the same reason, *Phaenicia* is a synonym of *Lucilia* (Stevens and Wall 1996). Many blowfly species are widespread in Africa (Zumpt 1956, 1965). *Chrysomya albiceps* is commonly found on carrion in most places; *Chrysomya putoria* and *Hemipyrelia fernandica* are more important in tropical Africa, and *Chrysomya chloropyga* dominates in temperate South Africa.

Because of their significance in forensic entomology, larvae and adults of most species can be identified by either morphological or molecular means (**Table 2**). The eggs of some species have also been described (Meskin 1991).

Aspects of the natural history of some species are covered by Ullyett (1950) and Meskin (1986). Studies of the development of African populations of several species are available (Richards *et al.* 2008, 2009c; Richards and Villet 2009), and non-African populations of some other species have been published (Ash and Greenberg 1975; Dallwitz 1981; Grassberger and Reiter 2001; Oliveira *et al.* 2007). Development is apparently correlated with latitude (Richards *et al.* 2008), and geographical distribution with humidity (Richards *et al.* 2009b). Studies of the mobility of African blowflies (Braack and Retief 1986; Braack and de

Vos 1990) show that at least some species can spread up to 60 km per generation, which explains why molecular studies have not yet found markers specific to African populations (Harvey *et al.* 2003, 2008).

6. Sarcophagidae (flesh flies)

There are about 200 species of flesh fly in Africa (Zumpt 1972; Pape 1996), placed primarily in the genus *Sarcophaga*, although some authors treat the subgenera as genera. Significant species include *Sarcophaga africa* (= *haemorrhoidalis*), *S. argyrostoma*, *S. aegyptica* and *Wolfahrtia nuba* (Tantawi *et al.* 1998). It is easier to identify males (base on their genitalia) than females, and larvae are only poorly known (**Table 2**). Because most species are larviparous, there is usually no need to identify eggs. Studies of the development of a few African species are available (reviewed by Villet *et al.* 2006), but practically nothing is known of the natural history of most species. Meskin (1986) suggested that some species preferred carcasses of small vertebrates.

Coleoptera (beetles)

Carrion beetles belong to two suborders, Adephaga and Polyphaga, very roughly corresponding to the carrion guilds of predators and necrophages, respectively. The marked phylogenetic trends seen in flies are not as obvious in beetles, although the Staphylinoidea and Scarabaeoidea are particularly well represented in carrion communities. About two dozen families of beetles have been found in carrion (Prins 1984a, 1984b; Braack 1986; Tantawi *et al.* 1996; Ekanem and Dike 2010), but only ten families and about 90 species occur predictably. By comparison, 221 species of beetles belonging to 15 families have been recorded from South America (Almeida and Mise 2009).

The beetles found on dryer corpses can be identified using the keys provided in the stored-product literature (e.g. Hinton 1945; Gorham 1987), while a general key to larvae and adults of carrion beetles was published by Smith (1986). The key to South American families provided by Almeida and Mise (2009) is also useful, although few genera occur in both Africa and South America.

1. Histeridae (clown beetles)

Carrion histerids are generally small, black, ovoid beetles with elytra that expose the last two abdominal segments, elbowed antennae that are often clubbed, and heads that can be retracted into the thorax. Although there are potentially a few dozen carrion-associated African histerids, there is no modern, comprehensive taxonomic resource for their identification, and numerous synonyms are being discovered (e.g. Mazur 2008). Reference should be made to general keys (**Table 2**) in conjunction with studies of local faunas such as those of Namibia (Yélamos and Vienna 1995), Gabon (Yélamos 1992) and Senegal (Gomy 2004). Because the species that are attracted to carrion are easy to trap and tend to be synanthropic, they are fairly well known, and include members of the genera *Acritus*, *Atholus*, *Chaetabraeus*, *Chalcionellus*, *Hister*, *Hypocacculus*, *Pachylister*, *Paratropus* and *Saprinus* (Prins 1984a; Braack 1986).

Many other species are attracted to herbivore dung, and may be attracted to the carcasses of herbivores when the gut contents become exposed. Carrion-associated histerids are often also found in dung or rotting vegetation (Prins 1984a; Davis *et al.* 1988; Davis 1993, 1994; Krell *et al.* 2003; Bousquet and Laplante 2006). The life cycles of two American species have been described (Summerlin *et al.* 1981), and are probably representative of many carrion-associated histerids.

2. Staphylinidae (rove beetles)

These are elongated, flexible beetles with very truncated elytra that expose half of the abdomen. Although specimens are common in carrion (**Table 1**), little attention has been given to the taxonomy of carrion-associated rove beetles. At least some African species of *Aleochara*, *Erichsonius*, *Gabronthus*, *Oxytelus*, *Philonthus*, *Staphylinus* and *Xantholinus* are attracted by the presence of fly pupae on which they feed (Prins 1984a; Braack 1986).

3. Silphidae (large carrion beetles)

These beetles are among the larger species inhabiting carrion in Africa. They are dorsoventrally flattened, with clubbed antennae that are inserted on the dorsal side of the head, and fluted elytra that usually leave the apical segment of the abdomen exposed. Three species are known from Africa (Schawaller 1981, 1987; Prins 1983). *Thanatophilus micans* (= *T. caeruleoviridans*) is widespread in sub-Saharan Africa (Schawaller 1981), while *T. mutilatus* is endemic to southern South Africa (Schawaller 1981) and *Silpha punctulata* (= *S. capicola*, = *S. peringueyi*) appears to be associated with Afromontane habitats (Schawaller 1987) such as the South African fynbos (Prins 1984a).

The nesting behaviour, development and larval morphology of *Thanatophilus micans* have been reported (Prins 1984a; Midgley and Villet 2009), and Braack (1981) reportted on the visitation pattern of *T. micans*. Prins (1984a) has commented on the natural history of *S. punctulata*.

4. Dermestidae (hide and museum beetles)

Dermestids are oval-bodied and often have a fine pile or scales on their elytra. The larvae are typically long-haired. Species of *Dermestes*, *Attagenus* and *Anthrenus* are found on carrion in Africa (Prins 1984b). It appears that all of the species of *Dermestes* and *Anthrenus* now found in Africa were introduced to the continent. A survey of museum records and literature indicates that apart from the cosmopolitan *D. maculatus* (= *D. vulpinus*), at least *D. ater*, *D. haemorrhoidalis*, *D. peruvianus*, *D. frischii*, *D. gerstaeckeri* and *D. wittei* occur in Africa. While *D. lardarius* and *D. cadaverinus* were intercepted at South African ports (cf. Prins 1984b), they appear to be otherwise absent from the continent.

Prins (1984b) provided notes on the identification and biology of some of the larvae commonly present in southern Africa. Peacock (1993) and Zhantiev and Volkova (1998, 1999) provided useful keys to adults and larvae.

Dermestes haemorrhoidalis is more common in winter in South Africa, and *D. peruvianus* is also associated with birds' nests (S. Beck and J.M. Midgley, pers. comm.). Studies of the development of two species are available (Coombs 1979; Richardson and Goff 2001). The modifications that they produce in carrion have been described (Voigt 1965; Offele *et al.* 2007). Adults of *Dermestes* species tend to be diurnal visitors to carrion, taking up residence only in drier carrion (Braack 1981).

5. Cleridae (ham beetles)

The brightly coloured, somewhat hairy Cleridae are represented in African carrion insect communities by three small-bodied species of *Necrobia* that are cosmopolitan stored-product pests (Smith 1986; Gorham 1987; Rajendran and Hajira Parveen 2005). They are attracted to drier carrion (Braack 1981).

6. Ptinidae (spider beetles)

These small beetles look like spiders because of their deflexed heads, globular elytra and long legs and antennae. There are keys to the adults and larvae of synanthropic species (**Table 2**). The majority of African species occur in arid parts of southern Africa. Some of the indigenous species are apparently ant-associated, and the life cycles of African ptinids have not been studied.

7. Trogidae (hair beetles)

These beetles are medium-sized, generally dark and warty, with characteristically clubbed antennae. About 300 species are placed in this family, which is related to the dung beetles. The 70 or so species of Afrotropical Trogidae are placed in the genera *Trox* (with the subgenera *Trox* and *Phoberus*) and *Omorgus* (with subgenera *Omorgus* and *Afromorgus*). The scutellum of species of *Omorgus* is constricted along its anterior margin, unlike that of *Trox*. Most flightless species belong to the subgenus *Phoberus* (Strümpher and Scholtz 2009). There are species-level keys to the adults (**Table 2**). The scaraebiform larvae have well developed lateral ocelli that distinguish them from other scarab families.

Few studies have addressed the natural history of African hair beetles, but Scholtz and Caveney (1992) showed that species in desert areas were active at dawn and dusk, and hid during the heat of the day, and Braack (1981) found them more common on older carrion. Some species of *Omorgus* are also associated with carnivore faeces, especially if it contains hair (Endrödy-Younga 1982; Walter 1983; Krell *et al.* 2003).

8. Scarabaeidae (dung beetles)

Dung beetles are generally highly recognisable, although some of the carrion-associated species are slightly unusual shapes. Comprehensive keys to the African genera of this very large family are available (Davis *et al.* 2008), but there is no consolidated resource for identifying species. Fortunately, few species attend carrion (**Table 1**) and those that do also visit faeces (e.g. Krell *et al.* 2003). These particularly include certain species of the genera *Anachalcos*, *Epirinus*, *Onthophagus*, *Phaeochrous* and *Sarophorus* (Braack 1981, 1986). *Epirinus* has been taxonomically revised (**Table 2**).

Dung beetles are unlikely to breed in carrion unless it includes suitable gut contents (Prins 1984b; Hegazi *et al.* 1991; Davis 1994), and can be expected to be rare on carnivore carcasses. They also tend to visit carrion during the day (Braack 1981).

Hymenoptera (wasps and ants)

Only a few families of hymenopterans are common in carrion ecosystems, and most of them are parastoids.

1. Parasitica

Nine species of parasitoid wasps from four families are consistently associated with African carrion communities (**Table 3**), and many of them occur more widely. *Nasonia* (= *Mormoniella*) *vitripennis* is a parasitoid of fly puparia and its presence extends the period over which PMIs can be estimated (Grassberger and Frank 2003; Voss *et al.* 2009a). Early in the 20th Century, it was the only parasitoid of carrion flies that was found in surveys in South Africa (Smit 1931). The life cycles of a few species have been studied from a forensic perspective (Geden 1997; Grassberger and Frank 2003; Turchetto *et al.* 2003; Voss *et al.* 2009a).

2. Aculeata

Ants are often found on carrion, and are generally represented by *Pheidole megacephala* or *Dorylus* species, although others may occur (Braack 1986; Ekanem and Dike 2010). Two species of wasps and three of bees have also been reported (Braack 1986; Tantawi *et al.* 1996; Okiwelu *et al.* 2008). No coherent taxonomic patterns are apparent in this fauna.

Lepidoptera (moths)

Two tineid moths, the keratin-eating *Trichophaga swinhoei* and the well-known horn-boring *Ceratophaga vastella*, have been reported (Coe 1978; Braack 1986), but little is known of their natural history.

Other insects and mites

A variety of other arthropods occur on African carrion, including centipedes, millipedes, spiders, mites, woodlice, earwigs, crickets and cockroaches (Prins 1983; Ekanem and Dike 2010). Similarly, parasites such as ticks, fleas and lice may be present (Mumcuoglu *et al.* 2004). At the species level, they are not consistent members of the carrion community and do not breed exclusively in carrion, so their identification is usually not significant to forensic studies, although much more attention should be given to the mites (Frost *et al.* 2010; Perrotti *et al.* 2010). Follicle mites may occur on canine and primate bodies (Özdemir *et al.* 2003; Perotti and Braig 2010), and phoretic and parasitic mites of 26 families have been reported from adult trogid beetles and piophilid flies (Prins 1983; Philips 2009), and are also common on dung beetles. Numerous other mites have been found to be associated with carrion insects on other continents (Frost *et al.* 2010; Perrotti *et al.* 2010). In the case of the beetles, an average of 28% of individuals harboured mites (Philips 2009).

FUNCTIONAL COMMUNITY COMPOSITION

Inventories of African carrion communities (**Table 1**) make it obvious that they are very similar to the carrion communities of other continents at the family level, but distinctive at the level of species, even though many of the species are cosmopolitan. Fortunately, the strong phylogenetic trends underlying the ecological characteristics of the community members at the family level mean that any particular community contains ecological analogs or surrogates of members of other communities. For example, the ecological characteristics of *Chrysomya albiceps*, which occurs in Africa, Europe and South America, are very similar to those of its sister species *C. rufifacies*, which occurs in Asia, Australia and North America, and the two species are in many ways ecological surrogates of one another. It is therefore possible to generalise the ecological structure of terrestrial invertebrate carrion communities world-wide by describing it in terms of the ecological roles filled by the animals. These roles or functions are termed guilds.

In forensic entomology, the guilds of carrion insects are usually defined as necrophages, predators and parasitoids, omnivores, and adventive species (Smith 1986; Byrd and Castner 2010; Goff 2010). This functional classification is heuristic, and it reflects the interests of forensic entomologists very strongly: it is based on the significance of each organism as a source of evidence. For instance, the necrophages are fairly specifically linked to carrion habitats, and therefore provide reliable forensic evidence; insect predators and parasitoids usually have narrow host preferences focussed on abundant necrophages, and therefore also have well defined forensic significance; while omnivores will be less clearly linked to the dynamics of the carrion habitat; and adventive species have practically no forensically meaningful link at all. In addition to these categories, guilds can be defined for species that were present premortem and either stayed after death, or left the site.

Necrophagous species

Necrophages are essentially obligate carrion-eaters. They are the most abundant, well-studied and useful guild for estimating the age of a corpse because of their predictably-timed appearance in carrion. The principal members are the larvae of Calliphoridae, Sarcophagidae, Silphidae, Dermestidae and Trogidae. This functional group may be further divided into 'wet' and 'dry' feeders, which essentially distinguishes the fly and silphid beetle larvae feeding on moist, putrefying tissue from the beetle and moth larvae feeding on desiccated and keratinised tissues.

The 'wet' tissues include the muscles and internal organs, and are both nutritious and digestible to most non-herbivores, so that competition for them can be intense, promoting the very prompt colonisation of carrion by 'wet' feeders. The 'wet' feeder guild therefore tends to have r-selected ecological characteristics. An exception occurs in the Silphidae, where members of the Nicrophorinae show parental care. Nicrophorine beetles, which are known as sexton beetles and do not occur in Africa, specialise on the carcasses of small vertebrates and bury them, thus preempting the resource and excluding further competitors.

Because the keratin in hair, feathers and skin is indigestible to most organisms, it is a relatively persistent resource that provides a niche to a guild of specialists, such as Ptinidae, Trogidae, Dermestidae and certain Tineidae, that tend to arrive after the 'wet' feeders have removed the more digestible tissues. While this guild still faces the pressures of competition amongst its members, the poor nutritional value of keratin means that its members grow more slowly, thus increasing their risk of predation. Arriving later at carrion has the benefit that fewer generalist predators will be attracted to the carrion by its odour or the presence of abundant prey such as maggots. The biochemical characteristics of carrion therefore have ecological consequences that lead to the temporal partitioning of the carrion ecosystem for necrophagous invertebrates, which is useful in estimating PMIs.

Further subdivision of the 'wet' feeders is possible because some species colonise carrion very promptly while others arrive later in a 'second wave' (Smith 1986). The first-wave colonisers are usually Calliphoridae (e.g. Braack 1981), while the second-wave colonisers, which characteristically arrive a day or two later, are usually Sarcophagidae and *Chrysomya albiceps* (Coe 1978; Prins 1982; Braack 1981, 1986; Tantawi *et al.* 1996). The Sarcophagidae are ovoviviparous and larviposit on carrion, while the primary colonisers lay eggs that hatch a day or two after being laid. This means that the larvae of the primary and secondary colonisers appear simultaneously on carrion, which has been interpreted as a response in the secondary colonisers to competition. However, flesh flies more often colonise small carcasses that dry out faster than large ones, so that larviposition may be an adaptation to the pressure to complete development before the resource becomes unavailable. From either point of view, it is not clear why Sarcophagidae are not primary colonisers.

The occurrence of *C. albiceps* as a second-wave colonist is generally attributed to its maggots' peculiar characteristic of being facultative predators (and cannibals) of maggots (Coe 1978; Prins 1982). This habit ameliorates competition by turning competitors into a resource, and allows the competitors to predigest the carrion, saving the predator some metabolic costs. It also extends the availability and freshness of carrion-derived nutrients: blowfly maggots have assimilation efficiencies of about 80% (Hanski 1976; Putman 1977), which means that much of the carrion becomes stored in their tissues, where microbes cannot access it. By being in the second wave of colonisers, females of *C. albiceps* can ensure that prey will be available, and these females have been seen laying their eggs among those of other flies (Smith 1986).

From a forensic perspective, the primary wave 'wet' feeders are the best species for estimating PMIs from the progress of pre-imaginal development (i.e., from the age of eggs, larvae or pupae) because the lag between death and the onset of their breeding is minimal; they are commonly reported to arrive within an hour of the carrion becoming accessible (e.g. Tantawi *et al.* 1996). The longer a necrophage takes to arrive at carrion, the less accurate a development-based estimate of PMI will be (Villet *et al.* 2010). The life cycle of *Thanatophilus micans* (Silphidae) is longer than that of most flies, which means that it can be used to estimate longer PMIs (Midgley and Villet 2009).

Although blowflies are numerically dominant, they are not keystone species in the sense that decomposition will occur without them, if only through the activities of the 'dry' feeders and microbes. However, the process will be protracted and the community disproportionally depauperate (Payne 1965) because maggots provide other taxa with access to parts of the carrion such as stomach contents and are themselves a resource for other carrion-associated guilds.

Specialist predators and parasites

These species prey specifically on necrophages, and include the larvae and adults of Histeridae and some Staphylinidae, and adults of Silphidae (Prins 1983, 1984a; Braack 1986) and macrochelid mites (Braack 1987). Smith (1986: 13), following Payne's (1965) guild definitions, placed the larvae of *Chrysomya albiceps* (and *C. rufifacies*, and possibly also *C. villaneuvei* from Asia) and *Hydrotaea* in this guild too because their larvae become facultatively predacious in their 3rd-instar (and possibly also the 2nd), although they have many of the ecological characteristics of necrophages. Although adults of *Necrobia rufipes* and *Dermestes maculatus* may prey on maggots (Braack 1986), it is not a sufficient part of their diets to warrant a place in this guild. It has been suggested that facultative predators should be rather recognised as omnivores (VanLaerhoven 2010).

Several species of Hymenoptera (**Table 3**) and the larvae of some staphylinid beetles like *Aleochara* (Prins 1984a) are parasitoids of fly maggots or pupae.

Members of this guild are not well studied in Africa (or elsewhere), and their value in providing evidence to forensic entomology is under-explored. A preliminary consideration of the ecology of this guild suggest that it is will provide less precise evidence for estimating PMIs because the arrival of guild members at carrion is dependent on the prior arrival of the necrophages, so that two suites of variables are involved in the estimate rather than one. When predators and parasitoids breed at the carrion site, the development of their larvae offers an independent means to estimate the PMI, although their later start to breeding has disadvantages for estimating a PMI from their developmental stage (Villet *et al.* 2010). However, certain parasitoids offer the advantage that their life cycles extend beyond the eclosion of unparasitised hosts, which means that they offer a means to extend the time over which PMIs can be calculated from larval development. This applies particularly to *Nassonia vitripennis*, which parasitizes fly pupae (Grassberger and Frank 2003; Voss *et al.* 2009a).

Omnivorous species

Various omnivorous animals will feed on carrion opportunistically. For instance, ligaments and cartilages may be eaten by *Odontotermes zambesiensis* (Coe 1978), which normally feeds on plant litter. Other African examples include certain ants, bees, wasps, cockroaches and beetles (Coe 1978; Prins 1983, 1984a, 1984b; Braack 1986; Tantawi *et al.* 1996; Okiwelu *et al.* 2008; Ekanem and Dike 2010). If scavenging vertebrates are not excluded from the definition of the carrion community, they would predominantly fit into this guild.

Members of a second category of omnivore eat carrion and prey on maggots, e.g. some wasps, carabid beetles, and the army ants, *Dorylus* spp. In terms of vertebrates, at least 12 species of African bird feed on maggots opportunistically (Coe 1978), and scavengers like jackals (*Canis mesomelas*), which sometimes produce droppings containing maggots (pers. obs.), may inadvertently eat carrion insects along with carrion.

The members of this guild generally indicate little about the history of the corpse; ants and vertebrates in particular may even confuse evidence by disrupting both the carrion and the activity of necrophages (Campobasso *et al.* 2009). Ants may also remove bone chips from weathered remains (Coe 1978), and even giraffes regularly remove cleaned bones (e.g. Wyatt 1971). To emphasise their weak forensic relationship with carrion as well as their ecological role, this guild may be more accurately termed 'opportunistic scavengers'.

Adventive species

Spiders, myriapods and other insects may occur on or under carrion, using it for shade or shelter, or as a vantage point (e.g. robberflies: Asilidae) (Prins 1983; Braack 1986). For these animals, the carrion could equally well be a log or stone. Such animals are without intrinsic forensic significance because they are unpredictable visitors. However, they should not be ignored in investigations because their activity may provide evidence of the passage of time that is of forensic significance, essentially as a form of trace evidence. For instance, the presence of a completed spider's web on a corpse contradicted a defendant's testimony and contributed to their sentencing (Gifford 2005a, 2005b). Members of this guild may also help to associate corpses with places or suspects by providing trace evidence (Smith 1986; Lord 1990). What is important here is that the guild member is sufficiently narrowly distributed in time or space that its occurrence on a corpse (if the corpse was moved) or suspect can most plausibly be explained by contact at a particular time or habitat.

Incidental species

Practically any mobile terrestrial or airborne insect may land on carrion accidentally. Such specimens can potentially provide trace evidence that associates a person or animal with a particular place or suspect.

Pre-mortem species

Carrion may host ticks, lice, fleas and other parasites that were present before death, and which have not had sufficient time to emigrate (Smith 1986). They are forensically useful in that they can provide evidence of the recentness of the death of the host. In cases of drowning, ectoparasites may take far longer to die than their hosts, and the time it takes to revive them can offer an estimate of how long they (and by implication, the corpse) have been immersed (Smith 1986: 25).

The maggots of some carrion-associated flies may also be present before death, either because they are involved in parasitic myiasis (Zumpt 1965) or because they have colonised sores or soiled clothing or nappies of injured or neglected animals, children or the elderly (Benecke and Lessig 2001; Anderson and Huitson 2004; Cooper and Cooper 2008; Goff *et al.* 2010). Such insects can provide evidence of the minimum duration of criminal neglect of live victims, but complicate forensic analysis post mortem.

Absent and absconded species

Some organisms may provide forensic evidence by their unexpected absence: a variety of soil-inhabiting species, such as Collembola, leave the area of a corpse rapidly after its appearance, and return only slowly after it is removed (Smith 1986). The fluids that seep from carrion may percolate over a metre into sandy soils or pool on the surface of poorly permeable soils and soak in only a few centimetres (Coe 1978). When a corpse or carcass has been removed from a site, the presence of this nutrient-enriched zone may still mark the site. The absconded soil fauna may take many months to return, so that soil samples from the site and from neighbouring control sites may corroborate evidence of when and where the carrion was present.

Other absences are to be expected. Sometimes rarer species simply do not find a particular corpse, and the forensic significance of their absence is small. Similarly, many species may be absent simply because they do not occur in the relevant area or the contemporary season. For instance, this might explain the absence of silphid beetles at pig carrion in Nigeria (Ekanem and Dike 2010).

Other guild classifications

The classification of guilds described here is a standard description (Payne 1965; Smith 1986; Byrd and Castner 2010; Goff 2010) that is predisposed towards an evidentiary, forensic perspective on carrion. It is intended to provide a framework for understanding the carrion community, but it is not explicitly ecological and other authors have used different approaches. The foregoing discussion has illustrated that how guilds such as the necrophages can be subdivided into 'wet' and 'dry' feeders to increase their forensic and ecological informativeness; these subdivisions could be treated as guilds in their own right. Braack (1986, 1987) emphasised the diet of the invertebrates and their degree of association with carrion, dividing the necrophages into sarcophages, coprophages, dermatophages, keratophages and detritivores. It has also been argued here that there is heuristic value in renaming the omnivore guild as opportunistic scavengers.

These revisions are not simply declarative, but aim to incorporate some insight into the mechanisms underlying the functional unity of each guild. As such, they would move the concept of each guild from being largely descriptive to being more explanatory. For example, the ecological (and forensic) significance of the digestibility of carrion components and the risk of predation become far more obvious in a revised classification of guilds, and increases the predictive power of the classification. Of course, even such a classification remains heuristic, and other classifications may suit other purposes.

COMMUNITY DYNAMICS

Van Laerhoven (2010) provides an excellent overview of ecological theory in relation to carrion communities. The assembly of species into a community on a particular carcass or corpse is affected by a suite of mechanisms operating at different spatial and temporal scales. Spatial variation includes components such as geographical distribution and habitat preference (VanLaerhoven 2010).

The carrion community present at any instant changes over three time scales: circadian, annual and the duration of decomposition. Being ectothermic, most carrion animals are less active in colder conditions such as at night and in winter. The range of mechanisms affecting community dynamics over the lifespan of a carrion source is more complex.

Circadian variation

Braack (1986) showed that adults of a variety of flies and beetles are diurnal visitors to carrion. These species generally feed on carrion fluids and conduct the rest of their lives elsewhere, but some are also present to oviposit. Species with adults that feed on the solid parts of carrion tend to take up residence and shelter in the carrion overnight while it suits their needs. There is evidence of crepuscular activity in piophilids (Braack 1981) and trogids (Scholtz and Caveney 1992) in some climates. From an ecological perspective, environmental temperatures and light levels are implicated as the principal mechanisms driving circadian cycles (Villet *et al.* 2010).

The occurrence of circadian cycles in adult blowflies and flesh flies is important in forensic contexts because it constrains the hours when eggs can be laid, and this affects the estimation of PMIs. If an animal dies early in the evening, flies will probably not lay eggs on it until the next day, and an estimate of the PMI based on the development of the immature flies will need to take this disparity into account. Nocturnal oviposition has never been reported from outdoor sites in temperate climates, but there are several reports from tropical Asia (e.g. Singh and Bharti 2001, 2008) where nocturnal temperatures are higher, and this issue needs investigation in Africa.

Circadian rhythms also affect the timing of other activities of invertebrates, such as the migration of mature maggots from carrion and the eclosion of adults (Villet *et al.* 2010). This affects the accuracy of estimates of PMIs by 'norming' the timing of these developmental landmarks to particular times of day, and produces a variable bias and precision that limits the accuracy of such estimates (Villet *et al.* 2010).

Seasonal variation

Whereas circadian cycles have only minor influences on the presence of immature stages of carrion-associated species on a particular carcass, seasonal cycles affect whether a species breeds on it at all. The core membership of the carrion community is therefore more strongly affected by seasonal variation than by time of day.

Apart from its role in circadian rhythms, temperature apparently also regulates the seasonal occurrence of many carrion arthropods, producing changes in which species represents their guilds (Ullyett 1950; Braack and de Vos 1987). In South Africa, *Dermestes peruvianus* is more common in winter and *D. maculatus* in summer. *Calliphora croceipalpis* is characteristically active in winter, *Chrysomya chloropyga* in spring and *Chrysomya putoria* in later summer. In the case of the flies, these differences in seasonal occurrence are reflected in their thermophysiological tolerances (Richards *et al.* 2009a) and their geographical distributions (Richards *et al.* 2009b).

Two thermophysiological mechanisms can produce seasonality. Diapause certainly occurs in some African carrion insects (Denlinger 1978), so that adults are not available to colonise carrion in certain seasons. Other species may migrate into a region seasonally, becoming locally extinct in intervening seasons (Povolný 2002; Verves 2004; Rosati and VanLaerhoven 2007). Such migrations have not been reported in Africa, although indigenous blowflies are very mobile (Braack and Retief 1986; Braack and de Vos 1990; cf. Williams and Villet 2006). There is a possibility that the seasonal appearance of *Chrysomya putoria* in the Eastern Cape of South Africa is due to migration from further north.

An important subsidiary ecological mechanism producing seasonal variation in carrion communities is interspecific competition (Braack 1987; Tantawi *et al.* 1996; VanLaerhoven 2010). Direct interference competition occurs between dung beetles and *Musca* flies in the Kruger National Park: the beetles are inactive in winter and only then can the flies breed in rumen contents without physical interference (Braack 1987). In Egypt, predation by *C. albiceps* on *Lucilia sericata* apparently causes the latter to breed successfully in carrion only in cooler seasons, when *C. albiceps* is scarce (Tantawi *et al.* 1996).

The forensic implication of seasonal variation is that exuviae from the community found on carrion very late in decomposition can provide evidence of the time of year when the carrion was colonised. Examples were discussed by Smith (1986).

Decomposition-related variation

The source of the greatest variation in community structure is the decomposition process, which produces at least twice as much variation as seasonal extremes (Voss *et al.* 2009b: Fig. 2). The guild structure of the carrion community usually changes in predictable ways during decomposition (Braack 1987), forming an ecological succession (Smith 1986; Ellison 1990; Tantawi *et al.* 1996, 1998). Departures of this example of succession from the Clementian concept of succession have been pointed out (Braack 1987; Schoenly and Reid 1987). For instance, carrion usually lacks pioneering primary producers, its community dynamics conform strictly to neither a primary nor a secondary succession, and it is ephemeral (therefore lacks a climax or mature community). To acknowledge these differences, carrion decomposition was sometimes referred to as a 'microsere' (e.g. Johnson 1975), in the same spirit that the carrion community is referred to as a microcommunity. Modern interpretations of ecological succession have abandoned this Clementian terminology and its associated assumptions about what drives succession (Pickett and McDonnell 1989; VanLaerhoven 2010).

1. The decomposition process

The decomposition process is commonly described in terms of several successive phases or (micro)seral stages, usually based on the condition of the carcass. Some authors distinguish up to eight stages, while others stipulate only three, but then subdivide them (e.g. Coe 1978). Braack (1981) provided a table reconciling the stages described by four previous authors. The stages commonly mentioned in carrion studies are Fresh, Bloated, Active Decay, Advanced Decay and Remains (e.g. Tantawi *et al.* 1996; Byrd and Castner 2010; Goff 2010). The Fresh stage follows death immediately, and precedes the formation of significant amounts of gas trapped within the body cavity, which is characteristic of the Bloated stage. Once these gasses have leaked from the body, the carcass is actively decaying and insect colonisation has usually occurred. In Advanced Decay, fluids leak from the corpse and the remaining soft tissues desiccate to various degrees. Rain can moisten carrion in the Advanced Decay stage sufficiently that it returns to the condition of the Active Decay stage (Tantawi *et al.* 1996). Vertebrate scavengers can cause the elision of the Bloated and Active Decay stages, substantially depressing the numbers of insects that colonise the body (Coe 1978; Richardson 1980). Remains have little or no soft tissue and consist of bones, teeth and keratinous materials, and may be dispersed by vertebrates, including porcupines (Coe 1978) and giraffes (Wyatt 1971). Eventually the remains weather away through the effects of heat (which promotes fracturing and chemical reactions) and moisture (which promotes weathering directly and by encouraging microbes and algae).

Empirically, the stages grade into one another, and some of the transitions last longer than some of the stages (e.g. Braack 1981: Fig. 1). The transition from Fresh to Bloated depends on how promptly microbial activity within the body generates gas. The transition from Bloated to Active Decay is affected by how soon insects provide vents for the gasses by eating into the entrapping tissues, and is therefore associated with colonisation of the internal tissues by maggots. The transition from Active Decay to Advanced Decay is usually attributed to activities of insects that perforate the body and allow fluids to drain from it, and is anecdotally ascribed to the efflux of mature maggots when they are ready to pupate. The relative lengths of the Bloated and Decay stages depend in part on which species are present and in what numbers. For example, in Egypt in spring, the blowfly *L. sericata* dominates the Bloated stage in rabbit carrion, but in summer the flesh fly *W. nuba* fills this role. *Lucilia sericata* colonises in large numbers, and the carcass is soon perforated and passes into Advanced Decay stages, while *W. nuba* colonises in smaller numbers, leading to slower consumption of the carrion, protracted bloating and a later transition to Advanced Decay (Tantawi *et al.* 1996).

Because a mechanistic link is often made between the stages of decay and the activities of specific insects, it is regularly claimed in the forensic literature that each (micro) seral stage has its own community. However, empirical qualitative examination of published African data (e.g. Braack 1981: Figs. 1-11; Braack 1987: Fig. 3; Tantawi *et al.* 1996: Figs. 1-5; Ekanem and Dike 2010: Figs. 2-5; cf. Smith 1986: Figs. 3-4) shows that the match between the stages and the occurrence of particular insects is erratic and the succession progressive rather than episodic. Some of this may be attributed to the fact that a typical example of carrion is not a homogenous habitat, since its physical extremities provide microhabitats that may be in different stages of decay to its core biomass (and to one another), thus blurring the putative seral stages. Besides this spatiotemporal heterogeneity, the carrion is never really in a stable state because the feeding activities of the community members are a persistent disturbance at the same time scale as the succession process. Quantitative examination of published studies from outside Africa (Schoenly and Reid 1987; Boulton and Lake 1988) has shown that the decomposition process is essentially a continuum, and that the apparent stages should rather be treated as milestones that have descriptive value only (Goff 2010: 15).

The weakness of this link is actually fortunate for forensic entomology because if it were strong, the composition of the carrion community would provide evidence of the stage of decay only, but not of the age of the carrion, which is what is of most forensic interest; the stage can be determined simply by looking at the carrion itself! The continuous changes accompanying decomposition increase the temporal resolution, and therefore the forensic value, of succession as a 'clock'.

Tomberlin *et al.* (2010) suggested that a different way to describe the decomposition process is in terms of landmark events that are significant to the insects themselves. A phase of exposure follows death, ending when the body is detected by insects and the period of insect activity starts. This period can be subdivided into phases of detection, acceptance, consumption and dispersal, demarcated by location, colonisation and maturation of the insects, respectively. Similar terminology is used to describe the interactions between parasitoids, or herbivorous insects, and their hosts (e.g. Prokopy and Owens 1983; Quicke 1997). Because the durations of these phases will depend on which species is being considered (Tomberlin *et al.* 2010), this description is autecological rather than an account of the decomposition process or the carrion community. However, its components are important in explaining the place of each species in another process: ecological succession.

2. The ecological succession process

Even though the dynamics of carrion communities cannot be explained by a stage-based model of decomposition, there is a characteristic pattern of change that must be explained. The pattern involves initial colonisation of the carrion by primary and then secondary 'wet-phase' necrophages, followed by their predators and parasitoids, and as the soft tissues are consumed and the carrion dries out, the 'wet-phase' fauna leaves and 'dry-phase' necrophages become progressively numerically dominant, until only the strict keratophages are left to exhaust the resource. The occurrence of omnivorous, adventive and incidental species and the circadian rhythms of the necrophages form a kind of background noise to the pattern, which is bracketed by the absconded species. The initial influx of necrophages and their associated predators and parasitoids is rapid, and there is a steady and increasingly erratic attrition of the community as the carrion resource dwindles.

The species richness and diversity of the community are greatest around the transition from Active to Advanced Decay (Braack 1981), which can be conceptualised as an ecotone between the 'wet' and 'dry' carrion habitats. These habitats are differentiated along three interacting gradients (quality of nutrition, intensity of competition, and risk of predation) that are of significance to particular guilds, and which therefore affect the timing of occurrence of each species in the decay process and, consequently, the composition of the core carrion community at a given instant.

Dietary differences between species affect the rate at which their larvae can grow. Taxa eating abundant and digestible tissues will develop faster and disperse earlier than those that arrive at the same time but eat less nutritious tissues, creating the impression of a succession. For instance, *Thanatophilus micans* (Silphidae) can be present on carrion within 24 hr of death but its life cycle is longer than those of sympatric flies (Midgley and Villet 2008). Adults of *Trox* have been observed early in Active Decay, but their larvae are associated with late Advanced Decay and Remains. This represents the classical 'tolerance' mechanism of ecological succession (Connell and Slatyer 1977; Pickett *et al.* 1987; VanLaerhoven 2010).

Differences in dietary preferences also affect the cues that a species uses to detect carrion, and these cues arise from the carrion and its inhabitants at different but predictable points in decomposition. Carrion flies are attracted by sulphur-containing volatiles produced by bacteria (Bänziger and Pape 2004), particularly in the Bloated stage, while at least one parasitoid uses olfactory cues arising from an interaction between its prey and the carrion (Voss *et al.* 2009c), which means that its arrival lags that of its hosts. Specialist predators and parasitoids arrive only after their prey have colonised the carrion. Differences in the arrival times of blowflies and flesh flies might be due to the cues they use. Even many keratophages appear to use olfactory cues related to their diets, and adult dermestids, trogids and histerids are often present early in decomposition, feeding on wet carrion or maggots and building up reserves for breeding later. The arrival of one species contingent on the prior presence of another (e.g. maggots or bacteria) exemplifies the classical 'facilitation' mechanism of ecological succession (Connell and Slatyer 1977; Pickett *et al.* 1987; VanLaerhoven 2010).

Intraspecific competition between maggots is intense, but the significance of interspecific competition in African carrion ecosystems is debated (Ullyett 1950; Braack and de Vos 1987). Blowfly larvae excrete free ammonia, which is toxic to beetles and helps to exclude them in the early stages of decomposition. On the other hand, Putman (1977) showed that blowfly maggots are adapted to develop rapidly and that they can sidestep[1] intraspecific competition by maturing prematurely if needs be, leading to surprisingly low mortality (about 20% overall). Interspecific competition can be ameliorated by niche partitioning (VanLaerhoven 2010). In African carrion communities, this may involve preferences for different seasons, diets and carcass sizes (Meskin 1986). Within a particular carcass, partitioning can be produced by direct interactions or indirectly, through resource preferences. Larvae of *Chrysomya marginalis* (= *C. regalis*) are gregarious, large and very active, generating a great deal of metabolic heat, which creates conditions that apparently drive larvae of *Chrysomya albiceps* to outlying parts of the carrion (Prins 1982; Braack 1987). The 'dry' necrophages are adapted to different diets that require specialised handling techniques, thus partitioning the carrion. Trogid larvae even dig burrows into the soil near the carrion and line them with hair, pre-empting competitors and avoiding predators. Southern African flesh flies prefer small carcasses (Meskin 1986), while *C. marginalis* is rare on human corpses but appears to prefer large carcasses (Braack 1987), which may arise from a preference for olfactory cues characteristic of ruminant herbivores rather than omnivores (M.W. Mansell, pers. comm.). Because of their smaller biomass, small carcasses decompose faster than large ones, and experience a wider spectrum of physical conditions, so that species specialised on them must develop relatively rapidly across a wide range of temperatures. This seems to be the case in at least some flesh flies (Villet *et al.* 2006). The ecological significance of these phenomena is that necrophagous species apparently do not show strong direct interactions.

The direct interaction between predators (and parasitoids) and their prey is potentially much stronger. Larvae of *C. albiceps* may kill so many maggots of other flies that

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[1] The language used here is teleological, but should not be interpreted to mean that the organisms make intentional, strategic decisions.

they are sometimes the only species to reach adulthood (Prins 1982; Braack 1987). The timing of arrival of parasitoids in the succession depends on the prior presence of suitable larval or pupal hosts. The presence of some predators is less dependent on the presence of prey because they are facultative necrophages or because only their adults are predators, and they do not need to feed before they breed. Predation is not a dominant interaction in the 'dry' phase of succession. While it can be rife in the 'wet' phase, maggots minimise their exposure to it by developing very quickly. Because potential prey minimise their risk of predation and because predators have alternative feeding strategies, predation has only an inconsistent role in linking many members of the community.

Indirect interactions mediated via the carrion environment can also contribute to succession. The activity of maggots early in the succession generally helps to dry out the carrion, making it less hospitable to 'wet-phase' necrophages and more attractive to 'dry-phase' necrophages, which is a classical 'facilitation' mechanism (Connell and Slatyer 1977; Pickett *et al.* 1987; Schoenly and Ried 1987). It also decreases the risk of predation later in decomposition, providing a second mechanism of facilitation. However, the initial activity of maggots is neither necessary nor sufficient to produce the later stages of succession.

Over the last two decades, ecological succession has become understood as a product of many processes (including facilitation, inhibition and tolerance) that occur simultaneously or sequentially (Pickett *et al.* 1987; Pickett and McDonnell 1989; Viejo *et al.* 2008; Walker and del Moral 2008), and this perspective clearly applies to carrion community dynamics too (VanLaerhoven 2010). The community of the 'wet' phase of decomposition is dominated by r-selected species with dispersal characteristics adapted to colonizing a newly-formed habitat, and reproductive characteristics adapted to competing for a readily digestible resource and out-breeding predators. This phase is characterised by rapid change, instability and an emphasis on the autecology of each species. The 'dry' phase represents a more stable and enduring environment, with a community of more K-selected species that are partially recruited from the previous phase and specialised on various indigestible diets. They interact little with predators or each other. This phase is characterised by slow change, differential attrition of food sources, and an emphasis on each species' autecology rather than interspecific interactions. The emphasis on autecology in both phases is an example of the 'Law of Dynamic Tolerance' at work (Pickett and McDonnell 1989). The absence of suites of strong links between most species explains why the succession is not characterised by discrete waves of species (Schoenly and Reid 1987; Boulton and Lake 1988). The rate at which succession progresses depends on how many individuals inhabit the carrion and how active they are, both of which are affected by temperature. The degree to which a particular example of carrion conforms to the general pattern of terrestrial carrion succession depends on the extent to which it is dominated by disturbance (cf. Richardson 1987). Carrion experiencing more physical or climatic disturbance is likely to show increasingly idiosyncratic community dynamics and synecology. Fortunately, forensic entomology is usually interested in retrodicting the succession process of a specific case, so that the relevant conditions are more or less known and constrained.

3. Models for forensic retrodiction

The predictable succession of taxa during decomposition is forensically useful because it provides a clock for estimating PMIs. The challenge lies in calibrating it in the face of temperature-dependent variation in both rates of development of immature insects and the levels of activity of adult insects (on three distinct time scales).

The simplest approach is a pattern-matching technique called the Occurrence Matrix method (Schoenly *et al.* 1992, 1996). For any particular time, the presence of a species can be represented by a 1, and its absence by a 0. The structure of the community at that time can then be represented by a string of 0 and 1 symbols, where each symbol represents the occurrence of a particular species, which is always in the same position in the string. This string can be matched against a database of similar strings for different known points in the succession, collected under experimental conditions. The robustness of this method and a suite of complications are discussed by Schoenly *et al.* (1996).

The apparent paucity of strong ecological interactions between species that could produce discrete stages with the succession is advantageous for estimating PMIs because the community succession unfolds continuously, which increases the precision of the estimates. However, the pace of succession is temperature-related (Coe 1978; Braack 1986) because insects in warmer conditions are more active and more abundant (Smit 1931; Hepburn 1943a, 1943b; Mönnig and Cilliers 1944; Ullyett 1950; Braack and de Vos 1987) and their metabolism is faster. This means that carrion is found sooner and consumed faster in warmer seasons and even on warmer days. This effect can be accommodated by weighting the passage of time by the concurrent temperature (Michaud and Moreau 2009), a conceptual approach called physiological time (Villet and Amendt 2011). This method is also used in modelling the development of immature insects (e.g. Richards and Villet 2008). This approach effectively rescales the duration of each segment of the succession process so that it is measured on a relative time scale based on thermal units (usually degree-days). It has been used successfully to predict the time of arrival of five carrion insects in two seasons using logistic regression (Michaud and Moreau 2009). The model could be refined by giving attention to the thermal microhabitats occupied by each species on the carrion.

TROPHIC DYNAMICS

Decomposition recycles the nutrients and energy stored in an animal's body back into the environment. It was estimated that 10-20% or more of larger carcasses in natural tropical habitats were not found by vertebrate scavengers (Richardson 1980; Braack 1987), and these are recycled solely by invertebrates and microbes. As urbanization and rural development proceed, this proportion will increase as vertebrate predators and scavengers become scarcer.

Vertebrate scavengers removed the soft tissues of an elephant in three days (Curry-Lindahl 1961; Richardson 1980), a task that invertebrates could do in about 21 days (Coe 1978). Antelope carcasses may be stripped to bones by insects in about 5 days in summer, and 14 days in winter (Braack 1986). The keratinous parts of carrion are generally left by vertebrates and must be recycled by invertebrates and microbes. Nutrients in bones may take decades to weather out (Coe 1978), especially if they are kept dry and cool, but decomposition liberates those in other tissues fairly promptly.

Although Coe (1978) estimated that insects recycle only about 5% of the tissue of an elephant, other estimates place the proportion nearer 80%, with the remainder attributed to bacteria (Putman 1977; cf. Payne 1965). The net production efficiency of blowflies is about 80% (Hanski 1976; Putman 1977), which means that about 65% of a carrion source is converted into invertebrate biomass, and because these organisms are mobile, it is soon exported from the site. The remaining 35% of the carrion is either bone or excreta that leach into the soil of the site and result in islands of more vigorous vegetation (Coe 1978; Parmenter and MacMahon 2009).

Because invertebrates eat practically all of the soft tissue on a carcass, they will consume any contaminants in the carrion too, and these may be excreted, metabolised or stored in their tissues or their cuticles. Traces of some drugs can be detected in the exuviae of beetles (Miller *et al.* 1994), which are moderately tough, and may remain at a death scene long after the corpse has decomposed beyond toxicological analysis, thus providing a useful source of toxicological samples for forensic study.

Although rarely of forensic significance, carrion insects may also be involved in epidemiological processes, particularly the transmission of anthrax (Braack and de Vos 1990), polio and hepatitis (Zumpt and Patterson 1952), and in destroying diseased carcasses.

FUTURE DIRECTIONS

The carrion ecosystem therefore appears to host a weakly integrated community of ectotherms that are primarily concerned with feeding on a heterogeneous, ephemeral resource without being eaten themselves. Changes in the community are driven largely by conditions that are relatively easily measured or at least approximated. This perspective is exciting for forensic entomology because it makes the dynamics of the carrion ecosystem easier to model and to apply to criminal investigations.

A primary purpose of science is to increase the predictability of the world by providing natural explanations for phenomena. This enables humans to prepare for the future and (more significantly for forensic science) to explain the past. Predictability is ensured by generalising observations into theories, and the past is explained by understanding particular conditions in terms of such theory. Forensic science therefore draws on theories to interpret evidence, and the quality of those theories is therefore important to the realisation of justice. For these reasons, it is as important to forensic science as it is to science in general to move from purely descriptive understandings of phenomena to theoretical understanding (Tomberlin *et al.* 2010). In the case of carrion ecology, the most pressing areas for future forensic research are in understanding the colonisation process and understanding the role of pre-imaginal development of flies, beetles and parasitoids in the succession process (VanLaerhoven 2010: 511). Understanding the relationship between these processes and temperature has particular promise for forensics.

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