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Community dynamics of carrion-attendant arthropods in tropical african woodland

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Summary. Carcasses are temporary resources which are unpredictable and inconsistent in their availability and locality. A recognisable community of interacting user arthropods comprising sarcophages, coprophages, dermatophages, keratophages, detritivores, predators and parasites has evolved to exploit the carcass habitat. The large number of arthropods, close confinement, and limited duration of resources necessitates aggressive utilisation. The trophic relations, competition and successionary pattern of these arthropods is discussed. Several pathways to reduce competitive conflict are described. Succession at carcasses is viewed as being inherently different from the traditional concept as the habitat is non-replenishing and does not lead to a climax community.

Key words: Carrion – Savanna – Arthropods – Community

Sustained long-term functioning of most ecosystems depends in considerable measure on effective cycling of nutrients. Scavengers and decomposers of animal products play an important role not only in accellerating the return of nutrients to other constituents of the trophic web, but also disseminate such nutrients over a wide area, and contribute to the dilution of potentially infective disease foci from animals dead of such causes. The most noticeable of such scavengers in a natural tropical woodland area such as the northern Kruger National Park (KNP) are vultures, hyaenas and jackals, but insects are also highly effective in carcass degradation (Braack, 1981). Richardson (1980) and Braack (1984) indicated that especially in well-wooded environments up to 20% of medium- to large-sized mammal carcasses may remain undiscovered by vertebrate scavengers. Such carcasses are rapidly colonised by blow-flies and other insects which have the potential of removing all carcass soft-tissues within four days in warm weather. Only within recent years have studies been performed on this complex of arthropod species in Africa (Braack, 1981, 1986; Coe, 1978; Meskin, 1980; Prins, 1980, 1982; Richardson, 1980), although myiasis-producing blow-flies previously stimulated considerable research on calliphorid dynamics at carrion (e.g. Smit, 1929, 1931; Hepburn, 1943a, b; Mönnig & Cilliers, 1944; Ullyett, 1950). This paper will strive to elucidate the trophic relations, competition and succession of the carrion-attendant arthropod species in the KNP.

Methods

The studies upon which this paper is based were mainly performed in the north-eastern corner of South Africa in the Pafuri area of the KNP. It is a semi-arid region with an average annual rainfall of 438,1 mm (Gertenbach 1980), with *Colophospermum mopane* woodland predominating (Gertenbach 1983). Three full-grown impala rams (*Aepyceros melampus*) were shot in early January 1979 and placed individually in large-mesh fencing-wire enclosures to exclude vertebrate scavengers. Two of the carcasses were visited every six hours for the first 13 days after placement for total collections of all insects present (excluding larval stages such as blow-fly maggots), and thereafter every 12 h until Day 24, followed by irregular visits thereafter. At carcass B all beetles and other slow-moving arthropods were collected by handpicking, whereas a large tent-like net was used to collect flies and rapid-moving arthropods at carcass C. Carcass A was used as control to determine the possible effect on decomposition and succession of continuous collection at the other two carcasses. In this manner it was determined that the frequent collection of insects did not obscure or alter the pattern of succession or relative abundance of species, due to the rapid rate of recruitment and the large reservoir of carrion-arthropods in the area. Notes were made at each collection period of the habits and interactions of the various species, together with other relevant observations such as carcass-conditions. Six more impala were similarly used in May/June and September/October to determine seasonal fluctuation. Observations were subsequently made at more than 200 naturally-occurring carcasses throughout the KNP, which indicated that the same successionary sequence and relative abundances were valid under field-conditions as at the study-carcasses.

Results and discussion

The species composition, numerical abundance, diel visitation patterns, succession patterns, seasonal fluctuations and habits are fully detailed by Braack (1984) and summarised by Braack (1986). A total of 227 arthropod species in 36 families were recorded utilising the carrion habitat, and 98,68% of the species were of the class Insecta. The most abundant and consistent users of the habitat were (number of species in brackets) Histeridae (24), Trogidae (6), Scarabaeidae (46), Dermestidae (1), Cleridae (1), Piophilidae (2), Sphaeroceridae (12), Chloropidae (9), Milichiidae (5), Muscidae (21), Calliphoridae (20), Tineidae (1), Pteromalidae (1), Diapriidae (1), Formicidae (10), and Acarina (3), showing a clear predominance of Coleoptera and Diptera.

Trophic relations

It bears repeating that a carcass is not a single homogeneous entity as is conveyed especially by the term "carrion", but is composed of a number of clearly separable constituents which serve as attractant stimuli and feeding substrates. These include flesh, fatty deposits, fluids, rumen-content, skin, horn-sheaths and hooves, and each of these component units may serve as an independent source of attractant and resource for a group of user-arthropods. The carrion community is not described and defined by only the sum of the species attracted to these components but includes also the arthropods which are attracted to feed on or parasitise those insects feeding on the carcass.

In the following discussion on the carrion-community I have included only those species which are *regularly* attracted to carcasses in numbers considered *abundant* for the particular species so it can be regarded as a *concentration* of members. Some of these may be consistently and exclusively associated with carcasses, such as larvae of *Chrysomyia regalis* (= *C. marginalis*)[1] (Calliphoridae), *Ceratophaga vastella* (Tineidae), *Dermestes maculatus* (Dermestidae), *Necrobia rufipes* (Cleridae) and others, whilst some may be opportunistic, such as scarabaeids and ants. At herbivore carcasses, such opportunistic groups as scarabaeids are nevertheless *regularly* and *abundantly* attracted and must therefore be considered as part of the carrion community, despite the high likelihood that most scarabaeid species would be absent at a carnivore carcass.

Coprophagous will be used here to describe arthropods feeding on dung or components thereof; keratophagous those species feeding on horns and hooves, dermatophagous those feeding on skin, and those subsisting on fragmentary or particulate organic remains discarded by other organisms will be referred to as detritivores. The term necrophagous is defined in a biological dictionary (Kenneth, 1975) as meaning "Feeding on dead bodies" – which is not sufficiently specific as to components – while sarcophagous is stated as meaning "Subsisting on flesh". For our purpose "sarcophagous" will be regarded as the more appropriate term, and will be used in the sense of decomposing flesh and the film of moisture which often accompanies it and attracts some species of adult flies. For convenience blood will also be included in this latter category.

Some of the arthropods have feeding habits which cannot adequately be compartmentalised into a single category. Whereas blow-flies and piophilids for example, can be categorised as sarcophagous in the larval and adult stages, this is not possible for certain muscids and the scarabaeid *Anachalcos convexus* where the larval stages utilise dung but the adults prefer muscle tissues or their associated fluids. Similarly, dermestid adults may spend most of their time feeding on nearly-dry skin and ligamentous tissues, but they occasionally also scavenge on maggots caught by predatory beetles and at times even capture their own maggot prey. In this discussion, therefore, the species have been categorised according to their *preferred* source of nutrient intake where they spend most of their feeding time.

[1] Application has been made with the International Commission for Zoological Nomenclature to conserve the earlier name *Chrysomya marginalis* (Wd.)

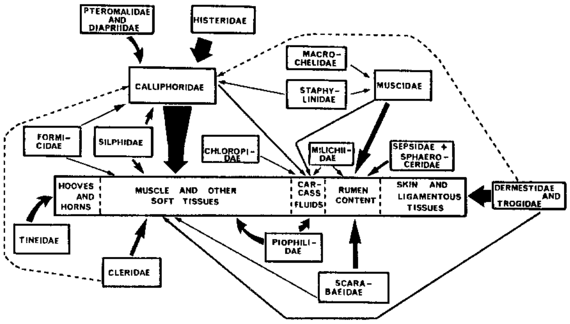

Fig. 1. Food-web of the main carrion-attendant arthropods in the Kruger National Park

The sarcophagous component

Carcass soft-tissues represent the most abundant of the food resources available at the carcass-habitat and supports the largest biomass of attendant arthropods. Of these the most numerous are calliphorid larvae which may number in excess of 210000 at an impala carcass (Braack, 1984). The blow-fly larvae, especially those of *Chrysomyia regalis*, are also the most important of the arthropods because of the influence they have on the carcass and as an abundant prey item for predatory members of the community. Although *C. albiceps* larvae are wholly dependent upon soft tissues in the first instar, they resort to opportunistic predacious behaviour in the second and third larval stages and prey heavily upon *C. regalis* larvae. Other species which rely either wholly or to a large extent upon muscle and other soft tissues are *Phaeochrous madagascariensis* and *Anachalcos convexus* (Scarabaeidae), piophilid larvae, silphid adults and larvae, *Ophyra capensis* (Muscidae) larvae, and larval and adult *Necrobia rufipes* (Cleridae). Ants occasionally also have opportunity to feed on the soft tissue component of the carcass, leaving a characteristic pitted appearance due to the removal of minute particulate portions of tissue. This generally occurs in winter when blow-fly activity is reduced; in summer ants rarely have opportunity to gain access to the carcass which is covered in a dense, highly active layer of maggots. Also included in this category are those arthropods which imbibe blood or the organic-rich fluids which bathe the tissues as a thin film, such as piophilid, muscid, chloropid and calliphorid adults.

In addition to forming the largest component in terms of biomass of the carrion-attendant complex of arthropods, the sarcophagous segment (effectively the larvae of *C. regalis*) also forms the pivotal basis for a considerable food-web which acts upon it. This food-web includes at least three additional trophic levels, namely predators, parasites, and detritivores.

The coprophagous component

This comprises essentially those species attracted to the rumen-contents of herbivorous mammals. Most belong to the family Scarabaeidae although *Musca* larvae (Muscidae) at times also utilise this resource heavily, especially where it exists in large quantity as at buffalo and elephant carcasses. Sphaerocerid, sepsid and milichiid flies similarly breed in dung or rumen-content, and the adults of these and *Musca*

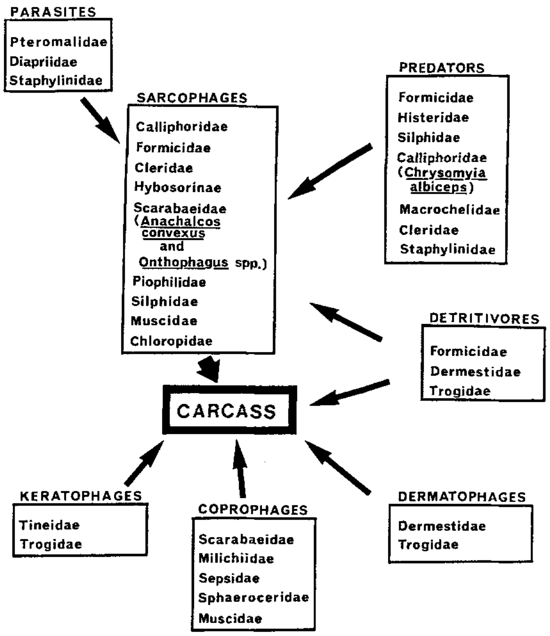

Fig. 2. Simplified representation of trophic interactions at the carcass-habitat, Kruger National Park

obtain nutrients from the liquid fraction. In the absence of blood or other carcass moisture, blowfly adults also readily imbibe rumen liquids. Generally the most numerous contribution to the coprophagous community is made up by the scarabaeid genus *Onthophagus* which may number many thousands of individuals at a carcass in summer.

The dermatophagous component

Despite its relative abundance at the carcass-habitat, skin is utilised almost exclusively by *Dermestes maculatus*, with a negligible portion consumed by trogid beetles. Although in excess of 3000 *D. maculatus* adults have been recorded at a single carcass, the larvae are mainly responsible for the complete consumption of this resource. Offered a choice, adult *D. maculatus* prefer moist muscle tissue and ligamentous remains to skin and subsist on fragmentary remains of these tissues to a large extent during their stay at the carcass. Adults occasionally also function as predators by preying on larvae of *C. regalis*, and frequently act as detritivores by scavenging upon the remains of dead insects around the carcass, especially blow-fly larvae left by predatory beetles.

The keratophagous component

As in the case of skin, the keratinous sheath of bovid horns and mammal hooves is a narrowly exploited resource which in the KNP is utilised only by the tineid moth *Ceratophaga vastella*, except for very minor consumption by trogid beetles. The paucity of species feeding on keratinous substances is due to the exceptionally high stability of the keratin protein and its resistance to proteolytic enzymes, making it difficult to digest. This aspect is discussed by Waterhouse (1957). Although a true member of the carrion-community which is exclusively dependent upon keratinous substances for its survival, *C. vastella* is rarely contemporaneous with any of the other community members because of its very late arrival at the carcass-habitat.

The detritivorous component

This group is represented by a few opportunistic species not always consistent or predictable in their pattern of attendance at the carcass. Most are ants which arrive soon after death of the animal and at least a few individuals are usually present at this habitat at any given time. They tend to be more numerous during the initial stage of decay when an abundance of carrion materials are available and numerous insects are present. They function both as predators by feeding on blow-fly eggs, larvae, and teneral adults, and as detritivores by utilising particles of organic offal. Of the ant species *Pheidole liengmei* was the most common.

Although more often encountered in its role as dermatophage, *Dermestes maculatus* displays great readiness to function as a detritivore by frequently feeding on the moist cuticular remains of *C. regalis* larvae partially consumed by histerid and other beetles, and will also feed on other dead insects.

The predacious component

The majority of species in the considerable assemblage of predators present at the carcass-habitat devote their attention to a single prey species, that being the immature stages of *Chrysomyia regalis*. Histerid beetles (at times more than 20000 per impala carcass) and the predacious 2nd and 3rd instar larvae of *C. albiceps* (up to 115000 larvae per impala carcass) account for the vast majority of mortalities amongst *C. regalis* larvae (Braack 1984).

Other groups which function permanently or temporarily as predators and feed not only on blow-fly eggs, larvae and teneral adults, but also on the immature and adults of other insects such as *Musca, Ophyra* and *Piophila*, are *Ophyra* larvae themselves, ants, silphids, and to a lesser extent clerids, dermestids, trogids, staphylinids and macrochelid mites.

The parasitic component

Aside from a few incidental individuals, the two main species present were *Nasonia vitripennis* (Pteromalidae) and *Trichopria lewisi* (Diapriidae). Both were found mainly in *Chrysomyia albiceps* puparia, although *N. vitripennis* was also collected from puparia of *Piophila* (Piophilidae). Examination of blow-fly puparia collected in different seasons showed that *T. lewisi* on average parasitised 5,17% of *C. albiceps* while *C. regalis* was not subjected to parasitism at all. This lack of parasitism in the latter species is related to the difference in pupariation behaviour, whereby *C. albiceps* lies exposed in a concentrated mass above-ground and *C. regalis* disperses and burrows into the soil prior to pupariation.

Although reputed to be parasitic on pupae of cyclorrhaphous flies (Voris 1934; Richards & Davies, 1977), no parasitism by species of *Aleochara* (Staphylinidae) was recorded, despite the presence of these beetles at the habitat.

Competition

Carrion is a temporary resource which is unpredictable and inconsistent both in its availability and locality. Because of the competition by vertebrate scavengers which use this resource, most invertebrate members of the carrion-community need to rapidly discover, colonise and maximally utilize the habitat. As the habitat rapidly fills with individuals and species, competition results between members utilising or searching for the same resources such as space, nutrients, and mating partners. Traditional competition theory (Hardin 1960; De Bach 1966) held that in the long term this should lead to the complete exclusion of some species sharing the same resources, or to the specialisation of species with acquisition of adaptations which render them competitively superior to other species in a particular portion of the habitat, or to partitioning of the resource so that the competitive interface is decreased (niche specialisation or differentiation). Current competition theory casts doubt on the true impact of competition, its ecological significance in the short term, and evolutionary significance in the long term. Uncertainty now appears to exist over the role of interspecific competition in causing niche separation in species having similar requirements (Thomson 1980; Haila 1982; Simberloff 1982). Connell (1980) indicated that no documented studies on competition have yielded conclusive evidence that niche specialisation among apparently competing species results from co-evolutionary divergence between the species. He believes rather that "... it is more likely that they diverged as they evolved separately so that, when they later came together, they coexisted because they had already become adapted to different resources or parts of the habitat". That competitive interfaces do exist, however, and that competition between species does occur, has been clearly shown in a wide range of field-studies (Connell 1983). Species having overlapping niche requirements have adaptations to maximise their effectiveness in utilising resources and minimising conflict. The carcass habitat is a particularly good environment to observe these species interactions because of the large number of individuals, close confinement, and the limited duration of resources necessitating aggressive utilisation.

Seasonal partitioning

Although species such as *Dermestes maculatus* are present and utilise the carcass-habitat throughout the year, there are other species which show a distinct seasonal peak and are replaced by another species utilising the same resource in another season. When referring to food requirements this is exemplified by the family Histeridae where members prey heavily upon *Chrysomyia regalis* larvae. The genus *Hister* tends to be abundant in summer but less common in winter when the numbers of *Saprinus*, especially *Saprinus cupreus*, are considerably elevated. A more clear example (although not applicable in the KNP as one species is absent) is the marked changeover in the use of carcasses by *Chrysomyia* larvae in the Cape Province and parts of the Transvaal. Here *C. regalis* utilises carcasses in summer to the near total exclusion of *C. chloropyga*, but the situation in reversed in the cooler winter months (Hepburn 1943; and unpublished work).

An example of combined food and space seasonal partitioning is afforded by the dominance of scarabaeids at rumen-content in summer when their activity – combined with that of blow-fly maggots – prevents the effective use of this resource for breeding by *Musca* flies. Scarabaeid activity is negligible in winter, and especially in late winter/early spring *Musca* flies capitalise on the opportunity thus afforded for breeding.

Carcass-size partitioning

There is evidence that some carrion-attendant species are adapted to more optimally utilise carcasses of a certain size-range, thus exemplifying another class of resource partitioning. Sarcophagids were never found breeding in any of the medium to large-mammal carcasses examined during the course of this study. On several occasions, however, I did find these flies successfully breeding in small carcasses such as mice and yellow-billed hornbill, without competition from *Chrysomyia* larvae. Denno and Cothran (1975) provided evidence suggesting that this is a widespread adaptation to minimise competition between sarcophagids and calliphorids. Working in California they found that of the flies breeding in rat carrion, 64% were sarcophagids, whereas in rabbit carcasses they formed only 2,8%. In a later publication Denno and Cothran (1976) found that, although calliphorids were competitively far superior to sarcophagids, species of these two families could coexist at rabbit carcasses in California, but with sarcophagids present only in very low numbers.

Observations at 304 small carcasses near Bredasdorp in the Cape Province convinced Mönnig and Cilliers (1944) that carcasses up to about 500 g attracted different flies compared with larger carcasses. Meskin (1980) found that *C. regalis* did not breed in small carcasses in the highveld region of the Transvaal, and he suggested that this species utilises larger carcasses for larval food resources. This is in agreement with the findings of Mönnig and Cilliers (1944) and my own findings in the KNP, so that collectively the evidence strongly suggests that some species have preferences for specific carcass sizes, serving to lessen competition between species having the same nutritional requirements.

Within-carcass partitioning

Interspecific competition amongst member-species of the carrion-attendant arthropod community for the same food resource appears minimal upon initial examination as most species utilise discrete non-overlapping resources and have differing strategies of carcass utilisation. Calliphorid, piophilid and muscid adults, for example, all feed on moisture at the carcass but avoid direct competition by having a preference for specific fluids and reaching abundance at different times in the decay sequence. Blow-fly adults are first to arrive and prefer the fluid-blood component. Piophilid and muscid adults arrive some days later but *Piophila* prefer the thin layer of moisture present on the carcass soon after *C. regalis* larvae have swarmed over the carcass. *Musca* also feed on this moisture, blood, and especially fluid-drenched rumen content and soil around the carcass, but *Piophila* has a tendency to be crepuscular and nocturnal whereas *Musca* has distinctly diurnal activity peaks. In a similar manner *Dermestes maculatus* has a strong and narrow feeding preference for skin and moist fleshy or ligamentous tissue, and *Trox* spp decrease the potential competitive interface with this dermestid by having a wider resource selection enabling them to feed with apparent equal facility on skin, suet, hooves, and general organic offal including freshly killed blow-fly larvae. Many other members of the carrion community can be shown to have specific non-overlapping preferences, such as tineids feeding almost exclusively on the horns of bovids.

Some apparent anomalies do exist. The two species *Piophila casei* and *P. megastigmata* have the adults overlapping entirely in their visitation patterns at the carcass and appear to have the same nutrient preferences. Although abundant, *P. casei* is nevertheless significantly less numerous than *P. megastigmata* but persists at the carrion-habitat for a slightly longer period. With both species feeding in the adult stage on moisture at the carcass, it appears the resource is under-utilised and sufficient to support both species simultaneously. Rather than provide an answer, however, this prompts the question why the resource is not more fully utilised by more *Piophila* adults. It seems likely that the adults are relatively free of limiting factors, but that the larval stages are subjected to severe resource limitations and are unable to produce a large adult population which can fully exploit available resources. The available evidence supports this latter possibility as *Piophila* larvae at medium-sized carcasses such as impala are restricted to very small pockets of resource left by calliphorid larvae.

Resource competition is not restricted to food however. An interspecific competitive interface may exist between species utilising different feeding substrates but require overlapping space, such as when larvae of *Chrysomyia regalis* swarm over the carcass during the latter stages of growth and prevent adult flies such as piophilids, *Musca* and *Ophyra* from settling to feed on moisture, additionally preventing coprophagous species from reaching the rumen content.

Interspecific conflict occurs between carrion-frequenting species of *Chrysomyia* and it is tempting to state that this conflict resulted in character displacement, which describes the acquisition of features by two competing species to utilise slightly different aspects of a niche and so reduce competitive conflict (Brown and Wilson 1956). In controlled studies it has been shown that when allowed to exist as isolated populations, *C. regalis* and *C. albiceps* larvae have the same preferred feeding sites at a carcass, but that under natural conditions where both utilise the same carcass *C. albiceps* larvae are actively excluded by those of *C. regalis* (Braack, unpublished work). At the carcass-habitat, *C. regalis* is generally first to arrive and oviposit, and this advantage together with an inherently larger size and vigorous activity ousts the later *C. albiceps* larvae from the carcass-body itself to peripheral areas where they feed on draining carrion-fluids and less attractive carcass components such as the limb-extremities. Both *C. albiceps* and *C. regalis* are sarcophagous in the 1st larval instar, but *C. albiceps* becomes a facultative predator upon *C. regalis* larvae in the 2nd and 3rd larval stages. It is not difficult to see how this could have been a secondary adaptation in response to severe competition by larvae such as those of *C. regalis*, resulting in character displacement to relieve the competitive pressure.

A different form of intraspecific competition exists in *Dermestes maculatus* (Coleoptera) where the potential for mortality-inducing feeding-conflict between adults and larvae is reduced by the adults having an earlier abundance period and a preference for moist muscle or ligamentous tissue-remains left by blow-fly maggots. The larvae – no doubt left no alternative but nevertheless doing well on this fare – subsist upon skin and are most numerous when most of the adults have departed.

An interesting phenomenon which does have a bearing upon intraspecific competition is the delayed period of peak abundance of *Chrysomyia regalis* males feeding at the carcass relative to that of females. This may have adaptive value as females have a more urgent requirement for a protein-rich meal necessary for proper ovarial development and production of viable eggs (Dethier 1976; Bowden 1982). The segregated periods of abundance are not likely to result from direct conflict as in the traditional concept of intraspecific competition, but could have been selected for due to the reproductive benefits which accrue. The same phenomenon of initial female preponderance has been observed in *C. albiceps* but not in *Ophyra capensis* (Muscidae).

Intraspecific competition among parasites, such as *Nasonia vitripennis*, can also be considerable. Cornell (1978) indicated that female *Nasonia* wasps tend to avoid ovipositing in fly-puparia already parasitised and, especially in areas such as Swellendam (Cape Province) where up to 47,56% parasitism of *Chrysomyia albiceps* puparia has been recorded (Braack 1984), such competition for suitable hosts is high. This competition, on a lesser scale, can also be expected to be operative in the other wasp, *Trichopria lewisi*, which regularly parasitises *C. albiceps* in the KNP.

Competition in the blow-fly guild

Competition between blow-fly larvae is a complex phenomenon influenced by such factors as the species involved, number of larvae of each species, difference in time between oviposition of the species involved, quantity of food available, environmental temperature, and most likely several other as yet undetermined factors. Two apparently similar carcasses can be placed alongside each other and be exposed to the same external environmental factors, and yet the eventual total numbers of larvae and their proportionate make-up will differ – often drastically (Braack 1984) – leading one to conclude that a considerable element of chance is involved.

Chrysomyia regalis adults arrive before *C. albiceps* in the successionary sequence of carrion-flies and are first to oviposit. The larvae, especially in the third instar, are extremely vigorous, tenacious, and swarm over the carcass.

The vigorous movement of *C. regalis* larvae, combined with their size advantage due to earlier oviposition and an inherent larger maximum size, results in the more sluggishly-moving *C. albiceps* larvae being unable to gain a hold on the carcass itself except at a few isolated positions, generally on the limbs. *C. regalis* larvae almost invariably occupy the carcass body itself, while *C. albiceps* arrange themselves along the periphery and, generally during the latter stages of growth, as a wide swath around the carcass. Often all the larval stages of *C. albiceps* will feed on carrion fluids soaking the soil and can frequently be found in organic fluid-pools. The 2nd and 3rd instar stages also prey to a considerable extent upon *C. regalis* larvae falling to the ground or crawling through the layer of *C. albiceps* along the periphery.

As revealed in related studies (Braack 1984) and also indicated by Ullyett (1950) and others (e.g. Levot et al. 1979; Bennettova and Fraenkel 1981), a manifestation of both inter- but more specifically intra-specific competition was a reduction in the average size of larvae at pupariation. The mortality rate was decreased by allowing successful pupariation in smaller, less well-fed maggots which yielded sub-sized adults. In controlled experiments Ullyett (1950) found that the fecundity of such undersized flies was reduced, but that, although less eggs were deposited by such flies, the eggs were nevertheless equal in size and viability to those produced by normal full-grown flies. They "... give rise to larvae which are healthy, are of normal size and which will, given the opportunity, produce pupae and adults which tend to conform to the mean maximum size for the species" (Ullyett 1950). My own studies (Braack 1984) confirm the results obtained by Ullyett. With increased competition, however, or with the premature removal of carrion-material by vertebrate scavengers, the nutrient intake may be insufficient for the formation of pupae, resulting not only in a reduction of average size but also reduction in numbers.

Succession

It has long been known that a pattern of sequential utilisation of resources exists at carcasses. The consistent and predictable nature of this phonomenon is such that it has been applied in criminal law situations to determine the amount of time elapsed since death by examining the organisms present at the cadaver (e.g. Mègnin 1894; Nuorteva 1977; Prins 1980). Many workers have commented on succession at carrion (e.g. Fuller 1934; Bornemissza 1957; Reed 1958; Payne 1967; Johnson 1975; Smith 1975; Braack 1981; Jiron and Cartin 1981) but other than an account of the sequence of species attendance, few (e.g. McKinnerney 1978) have made any significant analyses or theoretical contribution to the understanding of carrion succession.

All species of arthropods encountered at carcasses in the KNP had preference periods for attendance at the habitat when they reached maximum abundance, being absent or present only in low numbers at other times. These periods of abundance or maximal attendance for nearly all species may be short-lived or of long duration depending on the availability and condition of the food resource. For example, adult blow-flies, which feed on blood and other moisture and also oviposit at the carcass, were present for a short period lasting only a few days. By way of contrast trogid beetles, which have a wide resource selection including moist muscle tissue, suet, skin, hooves and even preying on blow-fly larvae, are present at the habitat for a very long time. Most species, however, have a peak preference-period which is of short duration.

Despite the seeming array of resources available at the carcass-habitat, there is little doubt that the presence of blow-flies – especially *Chrysomyia regalis* – is of central importance to the carrion-insect complex, and a crucial determinant of community structure. A large number of species depend either directly on the blow-fly larvae as a food-source or indirectly on the influence of maggots on the carcass. The activity of the maggots not only has a tremendous accelerating effect on carcass decomposition, but their effects – such as providing organic-rich liquids by secreting digestive enzymes which dissolve muscle and other soft tissue, by opening up the carcass, by leaving strands of ligamentous and other tissue which rapidly dry, etc. – additionally provide a wide range of different species with their particular food and space requirements. The presence of maggots, therefore, and their duration of stay, is a prime factor in determining succession at carcasses.

Chrysomyia regalis flies are almost invariably the first to appear at the carcass and oviposition by females soon follows, with adult *C. albiceps* following a very similar but slightly delayed pattern. Ants are also early arrivals which utilise blood or moisture oozing from body cavities, prey on blow-fly eggs, and later prey on larvae or feed on organic detritus at the carcass. With the emergence of blow-fly larvae, a large number of mainly histerid beetles arrive as predators and are soon joined by staphylinid and silphid beetles. With the moult to the second instar, numerous predatory larvae of *C. albiceps* join the attack on *C. regalis* larvae. As *C. regalis* larvae travel over the carcass abandoning exhausted feeding sites and seeking other sites, they leave an abundant supply of nutrient-rich moisture which is utilised by large numbers of piophilid, milichiid, chloropid and muscid flies. When maggots disperse to find pupariation sites they are again attacked by ants previously unable to reach the seething mass on the carcass. Pupariation in *C. regalis* generally occurs on Days 5 and 6 in summer and Days 9 to 14 in winter. This event marks the end of the most intense period of activity at the carcass and also a steep decline in the number of species present at the carcass. Pupariation of *C. albiceps* commences a day or two later and signals the arrival of diapriid and pteromalid wasps which parasitise *C. albiceps* puparia above-ground. With the emergence of blow-flies from their puparia a few days later, ants become abundant again to opportunistically capture any flies not rapid enough in their escape from the protective puparia.

Whilst the above sequence is in progress, and to a large degree independent of calliphorid activity (except in competition for space where blow-fly larvae at least temporarily prevent them from reaching their resource) the rumen-content component of the carcass also attracts a series of scarabaeid beetles, milichiid, sepsid, sphaerocerid and muscid flies.

As more and more of the carcass surface becomes exposed due to maggots moving to the inner recesses of the carcass to obtain fast diminishing resources, moist tissue-remains become available and the number of dermestid and clerid beetles increase rapidly. Dermestid adults deposit eggs and as the carcass dries after departure of the blow-fly maggots, so these beetles also steadily depart. The dermestid eggs soon hatch and larvae feed on the now near-dry skin. Trogid beetles remain common at this stage to scavenge on organic remains. Although not visible, parasitic diapriid and pteromalid wasp-larvae develop in many of the *C. albiceps* puparia long after the remainder have yielded adult blow-flies.

The last member of the successional sequence is the tineid moth *Ceratophaga vastella* which oviposits in the horns of bovids, arriving several weeks or even months after death of the animal. The larvae reveal their presence by the characteristic frass-studded silken tubes which protrude from the keratinous horn-sheath.

The above is a generalised account of the sequence of events which characterises most carcasses in the KNP. Because of the rapid rate of development of *C. regalis* maggots in summer the sequence is condensed into a very short period. With cool temperatures slowing their metabolic rate in winter, the process is extended and the successional pattern more easily observed.

Succession at carrion to a very large extent results from the addition, not replacement, of species to the community present at the carcass. The addition of species arises from

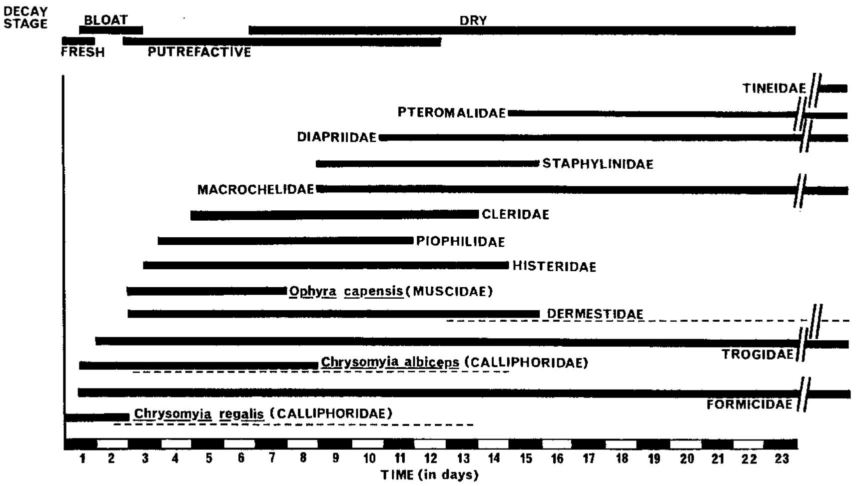

Fig. 3. Periods of peak attendance of the main carcass-frequenting arthropods during winter at Pafuri, KNP. Dotted lines represent larval stages. Visitation periods are of shorter duration during warmer months, obscuring the pattern of staggered arrival by different species/groups

new resources becoming available, and these resources most often in turn arise as a result of the action of one or more of the species members in the community. For example, the emergence of blow-fly larvae at the carcass stimulates the arrival of large numbers of predatory histerid beetles; the activity of the maggots leaves a liquid deposit on the carcass which attracts moisture-seeking piophilid and other flies; the continued feeding efforts of the maggots rapidly exposes the rumen-content in initially undamaged carcasses which is then utilised by scarabaeids; the departure of maggots creates space for more individuals of certain species such as clerids.

At the carcass-habitat the only resource items remaining available for a relatively long period of time are skin, hooves and horn-sheaths utilised by dermestids, trogids and tineids. The substrate is non-replenishing and is depleted in direct proportion to the population of arthropods it supports. Carrion therefore represents an ephemeral resource with no steady progression to a stable climax community having a reasonable prospect of long-term existence.

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