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 successional 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: Carcass – 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 accelerating 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; Mönig & 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 dominating (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 successional 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), Mus-
cidae (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 as 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) (Calliphoridae), Ceratophaga vestella (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, dermaphagous 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 catego-

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

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 wholly or to a large extent upon muscle and other soft tissues are Phaechroara 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. 1. Food-web of the main carrion-attendant arthropods in the Kruger National Park

rised according to their preferred source of nutrient intake where they spend most of their feeding time.

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