Arthropods associated with carcasses in the northern Kruger National Park

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Collections were made of arthropods attracted to nine freshly killed impala placed seasonally in vertebrate-excluding fenced enclosures. A total of 227 species in 36 families was found. No additional species were encountered in examinations of 107 naturally occurring vertebrate carcasses. The species are listed, together with their feeding preferences, habitat association, and maximum abundance per carcass. The blow-flies *Chrysomyia albiceps* and *C. marginalis*[a] were found to be important determinants of community structure owing to the dominance of the larvae in utilizing carcass soft tissues and the larvae serving as an abundant prey item. Arthropods were capable of reducing a medium-sized carcass to keratinous remains and bone within five days in summer and within 14 days in winter, without the aid of vertebrate scavengers.

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Nege vars rooibok-karkasse is in verskillende seisoene in omheinings geplaas en die Arthropoda daarheen gelok is versamel. 'n Totaal van 227 spesies in 36 families is gevind. Geen addisionele spesies is teëgekom by ondersoek van 107 karkasse onder natuurlike omstandighede. Die verskillende spesies word aangedui, sowel as hul voedselvoorkeur, verband met die habitat en maksimum getalle per karkas. Die brommers *Chrysomyia albiceps* en *Chrysomyia marginalis*[a] het 'n bepalende rol in die gemeenskapstruktuur van die Arthropoda weens die dominansie van die larwes in die benutting van die sagte weefsels van die karkas asook die beskikbaarheid van die larwes as prooi vir 'n wye verskeidenheid van spesies. Die afbrekingsproses deur die Arthropoda het daartoe gelei dat 'n vars karkas binne vyf dae in die somer en 14 dae in die winter gereduseer kon word tot keratienoorblyfsels en been, sonder hulp van gewerwelde aasvreters.

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[a]*Chrysomyia marginalis* is also known as *Chrysomyia regalis* Robineau-Desvoidy. Application has been made to the International Commission for Zoological Nomenclature for conservation of the name *Chrysomyia marginalis* (Wiedemann).

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Introduction

The role of decomposers in most ecosystems is of pivotal importance not only for the redistribution of available energy and nutrients but often also to limit the potential for disease outbreaks. Arthropods have a considerable role in this process because of their rapid location and complete reduction of carcass soft tissues (Fuller 1934; Payne 1965; Braack 1981). Even in undisturbed tropical systems it has been found that in excess of 10% of medium to large mammal carcasses may remain undiscovered or unutilized by vertebrate scavengers, where mainly arthropods then ensure effective decomposition of non-skeletal carcass components (Richardson 1980; Braack 1984). The ecological significance of such arthropods is likely to be even higher in countries or areas where human interference, by way of persistent hunting of supposedly vermin vertebrate scavengers which occasionally kill livestock, has resulted in a paucity of such vertebrate scavengers.

Although the species composition, successionary pattern and abundance of component members of the carrion-associated arthropod complex has been determined in many countries (Megnin 1894; Morley 1907; Fuller 1934; Chapman & Sankey 1955; Bornemissza 1957; Reed 1958; Payne 1965; Wasti 1972; Cornaby 1974; Nuorteva 1977; Jiron & Cartin 1981), this remains a poorly researched field and in Africa has only recently received attention (Coe 1978; Richardson 1980; Meskin 1980; Prins 1980; Braack 1981, 1984; McClain 1983). The present paper serves to detail the species encountered at collections made from more than 100 medium to large mammal carcasses in the northern Kruger National Park, South Africa, during a five-year study. Also indicated are their abundance, food relations and association with the carcass habitat.

Materials and Methods

A total of nine freshly killed impala (*Aepyceros melampus*) were placed in enclosures of wide-mesh fencing wire during January/February, May/June and September/October of 1979. The enclosures prevented disturbance by vertebrate scavengers, but allowed unimpeded access by arthropods (fencing mesh diameter 8 cm). Collections of all arthropods present at the carcasses, excluding larval stages such as blow-fly maggots and dermestid larvae, were made by dropping a tent-like net over the carcass to trap flying insects, whereas slow-moving arthropods were handpicked. This procedure is detailed in Braack (1981). The tent net trapped only those flying insects present on the carcass or in its immediate vicinity (1 m), so that the numerous flies resting on vegetation around the carcass are not reflected in the figures provided in Table 1.

Such collections were done every 6 h for the first 13 days, and at 12-hourly intervals thereafter until the 23rd day after placement. Irregular visits were then undertaken until only bone remained. All the arthropods collected were counted (excluding phoretic mites which were not found on carcass resources) and representative specimens forwarded to recognized specialists for reliable species identifications. Subsequent collections of arthropods at numerous naturally occurring carcasses of animals ranging in size from hares to elephant did not yield any species not encountered at the impala carcasses.

All observations were made in the semi-arid northern Kruger National Park (KNP) which has an average annual rainfall of between 438,1 and 587,8 mm (Gertenbach 1980), and average daily maximum and minimum temperatures of 29,4°C and 16,3°C (Van Rooyen 1978). Most of the study area is dominated by *Colophospermum mopane* woodland, described by Gertenbach (1983).

Results

These are detailed in Table 1. A total of 227 arthropod species

Table 1 Systematic listing of adult arthropods encountered at carcasses at Pafuri and their status within the habitat

Order / Family / Species	Greatest number per carcass	Season of greatest abundance	Food relations							Association with carrion habitat		
			Coprophagous	Sarcophagous	Dermatophagous	Keratophagous	Saprophagous	Predacious	Parasitic	Consistent	Opportunistic	Incidental
Dermaptera												
Anisolabis sp.	< 10						•	•				•
Bormansia meridionalis Burr	< 10	Summer					•	•				•
Euborellia annulipes (Lucas)	< 10						•	•				•
Hemiptera												
Reduviidae												
Fusius rubricosus (Stål)	< 10							•			•	
Lisarda rhodesiensis Miller	< 10	Summer						•			•	
Rhinocoris albopunctatus (Stål)	< 10							•			•	
R. violentus (Germar)	< 10							•			•	
Anthocoridae												
Xylocoris (Proxylocoris) afer Reuter	± 60	Summer						•			•	
Scutelleridae												
Solenostethium liligerum Thunberg var. *sehestedii* (Fabricius)	< 10	Summer										•
Coleoptera												
Carabidae												
Metagonum sp.	< 10							•			•	
Platymetopus curtulus Peringuey	< 10	Summer						•			•	
Xenodochus melanarius Boheman	< 10							•			•	
Histeridae												
Acritus apicestrigosis Bickh.								•		•		
A. infimus Desb.								•		•		
A. rugosus Bickh.								•		•		
A. serratus Burg.								•		•		
Atholus geminus (Er.)								•		•		
A. ruptistrius Lew.								•		•		
Chaetabraeus echinaceus (Schm.)								•		•		
Chalcionellus amoenulus (Fahrs.)								•		•		
C. splendidulus (Schm.)								•		•		
Hister gehini Mars.								•		•		
H. ignavus Farhs.								•		•		
H. tropicus Payk.	20 662	Late autumn						•		•		
Hypocacculus harmonicus (Mars.)								•		•		
H. metallescens (Er.)								•		•		
Pachylister caffer (Er.)								•		•		
P. nigrinus (Er.)								•		•		
Paratropus aptistrius Lew.								•		•		
Saprinus bicolor Fabr.								•		•		
S. cruciatus flavipennis Pering								•		•		
S. cupreus Er.								•		•		
S intricatus Er.								•		•		
S. rhytipterus Mars.								•		•		
S. splendens (Payk.)								•		•		
S. strigil Mars.								•		•		
Silphidae												
Thanatophilus (Chalcosilpha) micans Fabricius	265	Summer		•				•		•		

in 36 families were recorded using the carrion habitat, and 98,7% of the species were of the class Insecta. The most abundant and consistent families using the habitat were (with number of species given in brackets): Histeridae (24), Trogidae (6), Scarabaeidae (46), Dermestidae (1), Cleridae (1) (the foregoing 5 families all being Coleoptera), Piophilidae (2), Sphaeroceridae (12), Chloropidae (9), Milichiidae (5), Muscidae (21), Calliphoridae (20) (all Diptera), Tineidae (1) (Lepidoptera),

Table 1 Continued

Order / Family / Species	Greatest number per carcass	Season of greatest abundance	Food relations: Coprophagous	Sarcophagous	Dermatophagous	Keratophagous	Saprophagous	Predacious	Parasitic	Association with carrion habitat: Consistent	Opportunistic	Incidental
Staphylinidae												
Aleochara bohemani B. and S.									•		•	
A. punctipennis Bernh.									•		•	
A. quadripunctata Cam.									•		•	
A. trivialis Kraats									•		•	
Aleochara sp. 1, 2 and 3									•		•	
Atheta sp. 1 and 2								•			•	
Erichsonius sp.								•			•	
Gabronthus sp. 1, 2 and 3	625	Summer						•			•	
Philonthus? aemulus Tott.								•			•	
P. bisignatus Boh.								•			•	
P. cinctus Fauvel								•			•	
P. labdanus Tott.								•			•	
P. reinecki Schub.								•			•	
P. sp. cf. *minutus* Boh.								•			•	
Philonthus sp. 1, 2 and 3								•			•	
Trogidae												
Trox melancholicus Fahr.				•	•	•	•	•		•		
T. mutabilis Haaf.				•	•	•	•	•		•		
T. radula Erichs.	1 422	Summer		•	•	•	•	•		•		
T. rusticus Fahr.				•	•	•	•	•		•		
T. squalidus Ol.				•	•	•	•	•		•		
T. tuberosus Klug.				•	•	•	•	•		•		
Scarabaeidae												
Allogymnopleurus thallassinus Klug	< 30		•								•	
Anachalcos convexus Boheman	1 164		•	•	•						•	
Aphodius sp. 1 and 2	< 100		•								•	
Caccobius convexifrons Roth	< 30		•								•	
C. nigritulus Klug	< 30		•								•	
Catharsius philus Kolbe	< 30		•								•	
Copris amyntor Klug	< 30		•								•	
C. elphenor Klug	< 30		•								•	
C. evanidus Klug	< 30		•								•	
C. mesacanthus Harold	< 30		•								•	
Garreta nitens (Olivier)	< 30	Summer	•								•	
Gymnopleurus virens Erichson	< 30		•								•	
Metacatharsius opacus Waterhouse	< 30		•								•	
Milichus sp. probably *apicalis* (Fahraeus)	< 30		•								•	
Onitis fulgidus Klug	< 30		•								•	
O. granulisetosus Ferreira	< 30		•								•	
O. inversidens Lansberge	< 30		•								•	
O. obenbergeri Balthasar	< 30		•								•	
O. picticollis Fabricius	< 30		•								•	
Onthophagus (Proagoderus) dives Klug			•								•	
O. (P.) *rectefurcatus* Fairmaire			•								•	
O. aeruginosus Roth.			•								•	
O. anomalus Klug			•								•	
O. carbonarius Klug			•								•	
O. ebenus Péringuey			•								•	
O. gazella (Fabricius)			•								•	
O. herus Péringuey	5 670	Summer	•								•	
O. jeaneli D'Orbigny			•								•	
O. lamelliger Gerstaecker			•	•						•		
O. plebejus Klug			•								•	
O. sp. near *teitanicus* D'Orbigny			•								•	
O. vinctus Erichson			•	•						•		
O. sp. *fimetarius/leroyi* complex			•								•	

Table 1 Continued

Order / Family / Species	Greatest number per carcass	Season of greatest abundance	Food relations: Coprophagous	Sarcophagous	Dermatophagous	Keratophagous	Saprophagous	Predacious	Parasitic	Association with carrion habitat: Consistent	Opportunistic	Incidental
Pedaria sp.	< 30		•								•	
Phaeochrous madagascariensis Westwood	4 486			•			•			•		
Phalops ardea Klug	< 30		•								•	
Sarophorus costatus (Fahraeus)	2 304		•								•	
Scarabaeus ebenus Klug	< 30		•								•	
Sisyphus calcaratus Klug	< 30	Summer	•								•	
S. goryi Harold	< 30		•								•	
S. impressipennis Lansberge	< 30		•								•	
S. infuscatus Klug	< 30		•								•	
S. seminulum Gerstaecker	< 30		•								•	
Sybax distortus Schaum	< 30		•								•	
Tiniocellus spinipes Peringuey	< 30		•								•	
Dermestidae												
Dermestes maculatus De Geer	3 191	Late autumn			•		•			•		
Cleridae												
Necrobia rufipes (De Geer)	2 572	Summer		•			•	•		•		
Phloeocopus sp.	1	Summer						•				•
Nitidulidae												
Carpophilus nr. *quadrisignatus* Er.	< 10											•
Carpophilus sp.	< 10	Summer										•
Diptera												
Asilidae												
Bactria sp.	< 10							•			•	
Euscelidia rapax Westwood	< 10							•			•	
Hoplistomerus nobilis Loew.	< 10							•			•	
Neolophonotus (Lophopeltis) sp.	< 10	Summer						•			•	
Ommatius sp.	< 10							•			•	
Stichopogon caffer Hermann	< 10							•			•	
S. punctum Loew.	< 10							•			•	
Empididae												
Crossopalpus n. sp. near *aenescens*	< 10	Spring						•			•	
Phoridae												
Hypocerides spinulicosta Beyer	< 10										•	
Megaselia curtineura (Brues)	< 10										•	
Megaselia sp. near *pauculitincta*	< 10	Summer									•	
Plethysmochaeta sp.	< 10										•	
Sepsidae												
Australosepsis niveipennis Becker	< 50		•								•	
Paratoxopoda depilis Walker	97	Summer	•								•	
Xenosepsis sp.	< 50		•								•	
Piophilidae												
Piophila casei (Linnaeus)	5 849	Spring		•			•			•		
P. megastigmata McAlpine				•			•			•		
Lauxaniidae												
Cestrotus n. sp.	< 10											•
Homoneura (Keisomyia) n. sp.	< 10	Summer										•
Curtonotidae												
Curtonotum cuthbertsoni Duda	< 10	Summer										•
Sphaeroceridae												
Coproica demeteri Papp			•								•	
C. ferruginata Stenh.			•								•	
Coproica sp.			•								•	
Copromyza (Borborillus) marginatus Adams			•								•	
C. (B) sarcophaga Papp.			•								•	
C. (Gymnometopina) sp.			•								•	
Elachisoma braacki Papp			•								•	
Limosina (Bifronsina) bifrons Stenh.	223	Spring	•								•	
Limosina sp. 1 and 2			•								•	
Lotobia sp.			•								•	
Poecilosomella angulata Thom.			•								•	

Table 1 Continued

Order / Family / Species	Greatest number per carcass	Season of greatest abundance	Food relations: Coprophagous	Sarcophagous	Dermatophagous	Keratophagous	Saprophagous	Predacious	Parasitic	Association with carrion habitat: Consistent	Opportunistic	Incidental
Ephydridae												
Chlorichaeta albipennis (Loew.)	< 10										•	
Discomyza eritrea Cresson	< 10	Spring									•	
Mosillus beckeri (Cresson)	< 10										•	
Chloropidae												
Apotropina n. sp.	< 40										•	
Chloropsina sp.	< 40										•	
Conioscinella sp. 1, 2 and 3	< 40										•	
Oscinella sp.	< 40										•	
Siphunculina ornatifrons (Lw)	250	Spring					•			•		
S. punctifrons (Sabr.)	< 40										•	
Siphunculina sp.	< 40										•	
Milichiidae												
Desmometopa m-nigrum (Zett.)	< 40						•				•	
Leptometopa latipes (Mg.)	< 40						•				•	
Leptometopa n. sp.	< 40						•				•	
Meonura n. sp.	2 574	Spring					•			•		
Milichiella lacteipennis (Lw)	< 40						•				•	
Muscidae												
Atherigona aberrans Malloch							•			•		
A. naqvii Steyskal	1 289	Summer					•			•		
A. steeleae Emden							•			•		
Atherigona spp. indet.							•			•		
Fannia leucosticta Meigen	1											•
Graphomya leucomelas Wiedemann	1											•
Gymnodia mervinia	5											•
Gymnodia tonitrui Wiedemann	3											•
Haematobosca latifrons Malloch	1											•
H. spinigera Malloch	6											•
H. thirouxi ssp. *potans* Bezzi	7											•
Morellia nilotica Loew	3											•
Musca conducens Walker											•	
M. domestica ssp. *calleva* Walker			•	•			•			•		
M. domestica ssp. *curviforceps* Sácca and Rivosecchi	3 129	Spring	•	•			•			•		
M. lusoria Wiedemann												
M. sorbens Wiedemann											•	
M. xanthomelas Wiedemann											•	
Ophyra capensis Wiedemann	1 303	Spring	•	•			•	•			•	
Stomoxys sp. indet	1											•
Stygeromyia maculosa Austen	3											•
Calliphoridae												
Auchmeromyia bequaerti Roubaud	< 10								•			•
Bengalia sp.	< 10							•			•	
Chrysomyia albiceps (Wd.)	> 1 753	Spring		•				•		•		
C. chloropyga (Wd.)	< 10			•					•	•		
C. inclinata Walker	6			•								
C. marginalis (Wd.)	> 991	Summer		•						•		
C. putoria (Wd.)	< 10		•				•				•	
Hemigymnochaeta incerta Zumpt	< 10											•
H. unicolor (Bigot)	< 10											•
Hemigymnochaeta spp.	< 10											•
Lucilia cuprina (Wd.)	47	Winter		•					•		•	
L. sericata (Mg.)				•					•		•	
Rhinia apicalis (Wd.)	< 10											•
Rhyncomya forcipata	< 10											•
Sarcophaga haemorrhoidalis (Fallén)	< 10			•							•	
S. hirtipes (Wd.)	< 10			•							•	
S. nodosa Engel	< 10			•							•	
Stegosoma vinculatum Loew.	< 10											•
Tricyclea semicinerea Bezzi	< 10											•
Tricyclea sp.	< 10											•

Table 1 Continued

Order Family Species	Greatest number per carcass	Season of greatest abundance	Food relations: Coprophagous	Sarcophagous	Dermatophagous	Keratophagous	Saprophagous	Predacious	Parasitic	Association with carrion habitat: Consistent	Opportunistic	Incidental
Lepidoptera												
Tineidae												
Ceratophaga vastella (Zeller)	> 300	All year				•				•		
Hymenoptera												
Chalcididae												
Brachymeria podagrica (Fabr.)	< 10								•		•	
Pteromalidae												
Nasonia vitripennis (Walker)	< 40	Spring/ Summer							•		•	
Spalangia nigroaenea Curtis	2								•		•	
Diapriidae												
Trichopria lewisi Nixon	> 35	Spring/ Summer							•		•	
Formicidae												
Brachyponera sennaarensis (Mayr)	< 5 000						•	•			•	
Camponotus rufoglaucus (Jerd.) ssp. *zulu* Em.	< 300											•
Crematogaster castanea Sm.	< 5 000										•	
Dorylus fulvus Westw. spp. *badius* Gerst	> 15 000							•			•	
D. helvolus (L.)	< 5 000							•			•	
Megaponera foetens (Fab.)	< 100											•
Ocymyrmex weitzeckeri Em. *foreli* Arn.	< 5 000										•	
Pheidole crassinoda Em.	< 5 000			•			•	•			•	
P. liengmei For.	> 5 000			•			•	•			•	
Tetremorium pusillum Em.	< 5 000										•	
Sphecidae												
Bembix olivata Dahlbom	< 10							•			•	
Apidae												
Axestotrigona togoensis Cockerell	30 – 50						•				•	
Trigona (Hypotrigona) gribodei Magretti	30 – 50						•				•	
Acarina												
Acaridae												
Lardoglyphus sp.	< 100										•	
Macrochelidae												
Macrocheles muscae-domesticae (Scopoli)	< 100										•	
Pygmephoridae												
Pygmephorus sp.	< 100										•	

Pteromalidae (1), Diapriidae (1), Formicidae (10) (all Hymenoptera), and mites (3).

Resource utilization by the species enabled them to be grouped as sarcophagous, coprophagous, keratophagous, detritivorous, predaceous, or parasitic. Species differed in their degree of association with the carrion habitat, and three categories were selected to indicate habitat specificity. Species which were regularly attracted to carcasses in numbers considered abundant for the species and with no known preference for other habitat types (e.g. the blow-flies *Chrysomyia albiceps* and *C. marginalis*) were designated as being consistent users of carcasses. Those species which were attracted to carcasses because a particular resource was present but which also occurs in other habitat types were labelled 'opportunistic' species (e.g. dung-feeding scarabaeids). Species which were collected at the habitat irregularly and in very low numbers were considered 'incidental'.

All species were attracted to particular components of the carcass, or as predators and parasites to a narrow range of insects present at carrion. All species showed definite periods of peak visitation such that a sequential pattern of arrival and departure was exhibited, but this aspect, together with competition and other phenomena, will be discussed in a later paper.

Discussion

Of the various species of arthropods attracted to carrion, the blow-flies *Chrysomyia albiceps* and *C. marginalis* were found to be crucial pivotal species because of the ability of the immature stages to rapidly consume all carcass soft tissues, and by their presence and action on the carcass drastically influencing other members of the carrion community. The presence especially of *C. marginalis* larvae stimulated the arrival of large numbers of histerid and other predatory beetles, and their feeding activities made available nutrient-rich fluids and other resources (such as exposing rumen content) and thereby influenced the timing of peak arrival of insects such as piophilids, chloropids, milichiids, clerids, dermestids and also scarabs. The two species of blow-flies can be considered the most important determinants of community structure at the carrion habitat, directly and indirectly. Adult *Chrysomyia marginalis* blow-flies were the first arthropods to arrive at the carcass, within minutes in summer and generally within an hour in cooler months. *C. albiceps* was also an early arrival but peak attendance was consistently later than that of *C. marginalis*. In summer peak egg-deposition by *C. marginalis* occurred within the first 16 h after placement of the carcass, but in the colder winter months this was subject to considerable variation, sometimes occurring until Day 3. In *C. albiceps* peak oviposition occurred on Day 2 in summer and up to Day 6 or even 7 in winter.

At carcasses not utilized by vertebrates, blow-fly larvae were the first to make significant use of carcass material, excreting digestive enzymes which liquify the muscles and other soft tissues (Braack 1984). Although bacteria and other micro-organisms undoubtedly have a contributary and accelerating role in decomposition, Putman (1977) described experiments which revealed that blow-fly larvae consumed in excess of 80% of available carrion material. The extraordinary efficiency of food use by these larvae was also shown in the same paper by his finding that each larva consumed the approximate equivalent of $186,18 \pm 70,81$ calories which, when compared to the mean weight of a larva ready to enter the pupal stage converted to its calorific equivalent of 147,39, clearly indicates the exceptional efficiency of these larvae to assimilate and convert consumed material into body components as growth or reserves with minimal waste. Similar results were obtained in another study by Hanski (1976) who found that the instantaneous net production efficiency of *Lucilia* larvae during the intense growth phase varied between 79% and 84%. Payne (1965) compared the rates of decay of baby pigs exposed and unexposed to arthropod attack, and here the efficient and important role of insects as consumers of carrion was also clearly revealed.

In the warm climate of the Kruger National Park, blow-fly larvae were easily capable of reducing a medium-sized mammal such as an impala and even kudu to skin, bone and miscellaneous unutilized remains within five days in summer or within 14 days in winter. Other insects such as dermestids, trogids, clerids, tineids and scarabaeids soon removed carcass remains such as skin, fatty deposits, rumen-contents, and some keratinous material (e.g. bovid horns). By the combined action of these arthropods, an animal such as an impala could be reduced to bare bone and hair remnants within 47 days in summer, without the assistance of vertebrate scavengers. The disintegration process is considerably lengthened during the cooler months however, requiring double the time taken in summer or even longer.

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