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VISITATION PATTERNS OF PRINCIPAL SPECIES OF THE INSECT-COMPLEX AT CARCASSES IN THE KRUGER NATIONAL PARK

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Abstract — Two full-grown impala rams *Aepyceros melampus* were shot on 1978.01.07 in the Pafuri area of the Kruger National Park, Republic of South Africa. The carcasses were placed in enclosures 2,7 km apart and used to monitor the visitation patterns of insects. Collections of insects were made at four-hourly intervals for the first six days after placement of the carcasses, and thereafter every six hours up to the eleventh and final day. A figure is given to describe changes in the physical attributes of the carcasses through time. Twelve figures depict the patterns of arrival of insects at the carrion habitat. Species from the following families are represented: Cleridae, Dermestidae, Histeridae, Scarabaeidae, Silphidae, Staphylinidae, Trogidae (Coleoptera); Calliphoridae, Muscidae, Piophilidae, Sepsidae (Diptera); Diapriidae and Formicidae (Hymenoptera). The results indicate that species have distinctive periods of abundance and presents an overall picture of insect succession at carrion.

Introduction

Studies of carcass-visiting insect communities have been conducted in several countries, prominent examples being those done by Mègnin (1894) in France, Fuller (1934) and more recently Bornemissza (1957) in Australia, Chapman & Sankey (1955) in England and Payne (1965) and Wasti (1972) in the United States. With the exception of a study by Coe (1978) in which he discusses some of the insect species involved in elephant decomposition in Kenya, no publications appear to exist on the carrion-insect complex as a whole in Africa.

The study by Mègnin (1894) is generally agreed to be the classic work in the carcass-insect field. As he indicated, and most of the authors mentioned above have since verified, there is a recognizable pattern of insect species or groups of species which visit the carcass in a sequential manner, a phenomenon which has long been known as ecological succession. The most revealing study is perhaps that of Fuller (1934) who attempted "to study the carrion complex in Australia as an ecological unit — to discover the inter-relations and interactions of this association of insects".

The following study was conducted in the Pafuri area of the Kruger National Park, Republic of South Africa (22° 27′S 31° 17′E), from the 7-17 January 1978, and had as its aims:

1. to determine which insect species visit impala *(Aepyceros melampus)* carcasses;
2. in what numbers; and
3. to establish the general pattern of succession exhibited by these insects.

A complete list of the insect species found at the carcasses will be compiled for later publication, whilst the numbers and visitation pattern of the most abundant and important carcass-insects is provided here.

Material and Methods

Two rectangular wire enclosures (approximate dimensions: 2 x 3 x 2 m) were constructed in the Pafuri area using large mesh fencing wire (mesh diameter approximately 8 cm) and securing these around three Mopane trees *(Colophospermum mopane)* and several metal "droppers". The upper layers of the fencing were folded over to exclude entrance by vultures from above. Both enclosures had the bottom segment of fencing on one side untied but hooked to the fixed fencing to serve as entrance. The enclosures were situated 2,7 km apart (by road, in a fairly straight line), with both sites representative of the general habitat of the Pafuri area, this being fairly dense Mopane-veld with interspersed grass.

Potential insect dispersal range was kept in mind when siting prospective enclosure sites. In studies on a number of species of blow-flies, several authors (e.g. Lindquist, Yates, Hoffman & Butts 1951; Norris 1965; Schoof & Mail 1953; Yates, Lindquist & Butts 1952) have found that dispersion easily exceeds 2,7 km. However, some of the same authors, and others, also found that the majority of flies studied remained within a radius of 1 mile from a central point of release (e.g. Cragg 1955; Lindquist *et al.* 1951). The distance of 2,7 km between the two enclosures was therefore considered far enough to allow attraction either of insects from two populations or of different segments of the same insect population, *i.e.* one population would not be split in half, each half visiting a carcass, but the full numbers normally attending a carcass would still be attracted. This was assumed to apply to all insect species visiting the carcasses.

Two full-grown impala rams in prime condition (average mass approximately 65 kg, Labuschagne & van der Merwe 1966) were shot (head shots, minimal damage) between 07h30 and 07h50. The carcasses were placed, one per enclosure, within a few minutes of 08h00 on Day 1.

To simulate natural conditions to some extent it was decided to mutilate Carcasses B and C artificially as soon as this had occurred at Carcass A. An additional unfenced impala carcass open to vertebrate scavenging was placed 2,3 km from the nearest enclosed carcass. This was done at 12h30 on Day 1 by making one approximately 45 cm longitudinal and one approximately 30 cm transverse incision in the central region of the abdomen, these being the only mutilations besides the bullet holes in the head.

Two enclosure sites were used because of the different methods employed to collect insects attending the carcasses. At Carcass B only beetles and other insects reluctant to fly were collected. This carcass was placed on a doubled-up fencing-wire platform (approximately 1,0 x 0,75 m) so that the carcass could be lifted to facilitate collection of insects below. Even with the fencing-wire platform doubled several times the apertures were such as to allow insects an unobstructed access to and from the carcass. Collection was done by hand and at no time (except Day 11, when few insects were present) were there less than three people present to assist in the rapid-as-possible collection of insects. Insects were not only taken from the carcass itself but also from its immediate surroundings (approximately 1 m around carcass). Dry-cell torches and one or two fluorescent lights attached to a 12 volt car battery were used for night collecting. Flies were ignored at this carcass.

Diptera and other readily flying insects were caught at Carcass C, which was placed flat on the ground in its enclosure, using a large tent-like, very fine mesh, net (dimensions: L = 2,20 m, B = 1,27 m, H = 1,23 m; mesh diameter: 0,25 mm). The net itself tapered to a central point from which detachable separate bags could be attached. Night collection at this carcass was done by making minimal use of torches until the net had been dropped, since it was found that lights attracted flies very soon.

With the exception of the first two collection times, which were at 10h00 and 12h00 (Day 1, 1978.01.07), the collection of insects at Carcasses B and C was done at four-hour intervals for the first six days, and thereafter every six hours until Day 11. To remain as close as possible to these times, collection usually commenced about 15 min. prior to and finished about 30 min. after the stated times.

Another factor involved in the collection process deserves further explanation. As two of the aims of the project were to determine which insect species visit carcasses and their numbers, it was decided to make absolute counts of the insects at the carcasses. Absolute counts have the advantage that species present only in very low numbers would not be overlooked and the number of individuals per species would be reflected more accurately.

The method of handpicking insects at Carcass B served very well during the initial and end stages of the study period, but during the middle stages so many beetles were present at times that it became physically impossible for three people to collect them all. It thus became necessary to collect as many as possible for approximately 30 min., when each person would estimate, independently, what percentage of the total remained, the estimates would be averaged and that figure used as a correction factor.

Climate

First light and last light during the study period was approximately 05h00 and 19h00, respectively.

Unusually heavy rains were experienced in the area in 1977 and this continued into January 1978 immediately prior to the study period. Total rainfall in the study area for November 1977 measured 76 mm, whilst 264 mm was measured in December 1977. A further 25 mm fell on January 1st, 17 mm on January 2nd, 41 mm on the 3rd, 6 mm on the 5th and 8 mm on the 6th of January. It must be noted, however, that very slight intermittent drizzle fell on certain days during the study period which was unrecorded due to evaporation of the water in the rain gauge or simply insufficient to enable pouring off due to adhesion to the container walls. The heavy rains mentioned above would almost certainly have influenced insect populations, for the most part in a favourable manner. I have since conducted several similar studies at the same site and although the results have not yet been analyzed, it can be stated that certain insect species were present in particularly high numbers in the study recorded here, for example, staphylinids and silphids. However, a large decrease in the abundance of certain species has also become apparent, for example *Phaeochrous madagascariensis* has not exceeded about 10 individuals in total in the three subsequent study periods at the same site.

Measurement of ambient temperature (Table 1) was obtained from a shaded -20°C to +50°C mercury thermometer placed approximately 1,2 m above ground against a Mopane tree, near Carcass C.

Results

Decomposition of Carcasses B and C

The process of decay of organic material is highly complex with numerous interrelated factors influencing this process. Macroclimate, microclimate, availability of insects to aid in decomposition, extent of mutilations, are but a few of the factors involved in the decay process. To attempt to impose a standard series of clearly delimited stages of decomposition for carcasses, even under closely similar conditions, is therefore a very difficult exercise. It is thus not surprising that various authors, previously mentioned, have used different methods, parameters or "character-states", to delimit the various stages of decomposition. (See Table 1, Fig. 1 and Table 2).

As the various workers on carrion-communities tend to use different classifications of decomposition stages (Table 2), a combination and modification of some of the proposed stages were compiled for the purposes of the present study (Fig. 1). This was found necessary as decomposition was so rapid that certain stages suggested by the authors in Table 2 either overlapped or were so ill-defined as to make delimitation of their stages impractical and confusing. Nevertheless, it must be stressed that it is very difficult to determine accurately the beginning and end of each stage and the stages are therefore to a certain degree arbitrarily designated.

The stages of decomposition as given in Fig. 3 are based on notes taken on carcass-conditions at each collecting-time:

Stage 1 is given as "Normal Features" and this refers to the appearance of the animal when alive. It is not bloated, has no smell unless the observer is very close, the limbs are easily movable and the body exhibits normal resilience or "give" when pressed by hand.

Stage 2 refers to the carcass when bloated, normally first observed by the distended testicles and abdomen, and the animal is more solid or hard when touched, with little smell in evidence.

Stage 3 again refers to the bloated carcass, which embarks on a slow process of deflation and has a moderate to almost unbearable smell. In addition the body is very soft or spongy when pressed resulting from the liquefaction of the tissues.

Table 1

Weather observations made at Carcass C; rainfall measured at game-ranger's residence approximately 6 km from Carcass C

DATE	DAY	TIME	AMBIENT TEMPERATURE	GENERAL OBSERVATIONS	RAINFALL
			(°C)		
78.01.07	1	12h00 24h00	25,00 23,50	Overcast; windy Slight drizzle	1,5 mm
78.01.08	2	12h00 24h00	27,25 23,75	Overcast; slight breeze Overcast; slight breeze	Nil
78.01.09	3	12h00 24h00	24,00 22,00	Sight drizzle Some stars visible	Nil
78.01.10	4	12h00 24h00	29,75 23,00	± 40% cloudcover Starry sky	Nil
78.01.11	5	12h00 24h00	32,75 24,50	±70% cloudcover Starry sky	Nil
78.01.12	6	12h00 24h00	32,25 21,50	±75% cloudcover Overcast; very windy	13,5 mm
78.01.13	7	12h00 24h00	21,75 21,50	Overcast; windy Overcast; windy	Nil
78.01.14	8	12h00 24h00	27,50 18,75	±10% cloudcover Starry sky	Nil
78.01.15	9	12h00 24h00	29,75 19,75	±10% cloudcover No stars visible	Nil
78.01.16	10	12h00 24h00	30,50 19,00	±30% cloudcover Starry sky	Nil
78.01.17	11	12h00 24h00	34,00 24,00	±5% cloudcover Some stars visible	Nil

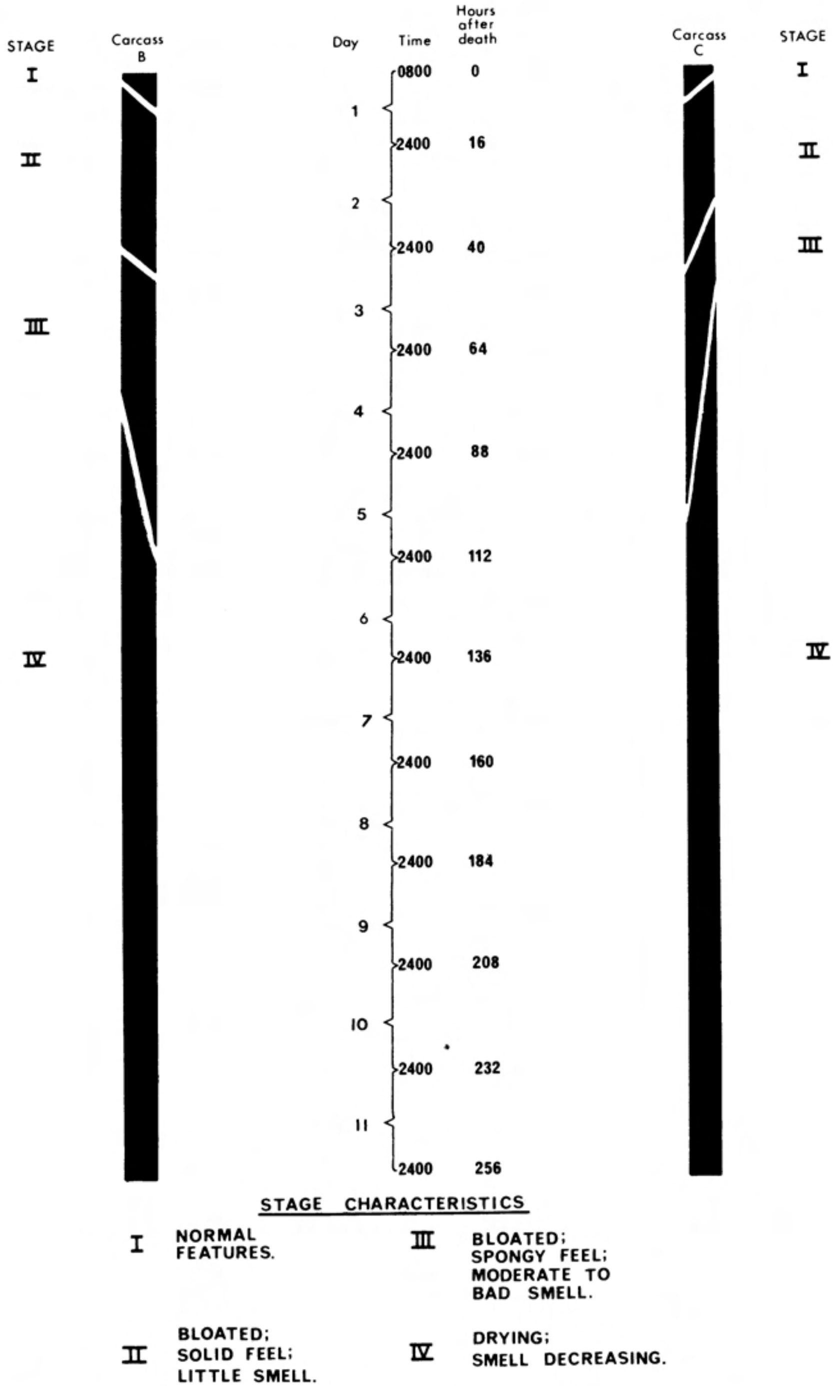

Fig. 1. Stages of decomposition of Impala Carcasses B and C, Pafuri, January 1978.

Table 2

Decomposition of carcasses on land as proposed by various authors

AUTHOR		STAGE 1	STAGE 2	STAGE 3	STAGE 4	STAGE 5	STAGE 6	STAGE 7	STAGE 8
MÈGNIN (1894), *in* Nuorteva (1977)		Bodies fresh	Decomposition commenced	Fatty acids	Gaseous products	Ammoniacal fermentation. Black liquefaction	Desiccation	Desiccation extreme	Debris
FULLER (1934)		Not smelling strongly	Active liquefaction & disintegration noticeable. Dipterous larvae and Coleoptera abundant	Drying of carcass with loss of smell					
BORNEMISSZA (1957)	Physical condition of carcass	Normal	Swollen by gases	Flat; flesh creamy	Flat; drying out	Hair and bones only			
	Stage of Decomposition	Initial decay	Putrefaction	Black putrefaction	Butyric fermentation	Dry decay			
PAYNE (1970)		Fresh	Bloated	Active decay	Advanced decay	Dry	Remains		

In Stage 4 the carcass has collapsed entirely, consisting almost entirely of skin and bone with little smell, and the drying process commences.

The number and species of insects visiting Carcasses B and C

A lengthy discussion of this topic is deemed unnecessary as the data are adequately summarized and presented in the various graphs, figures and tables (See Figs 2-13). However, a few comments on the more salient points are useful.

The numbers of individuals per species, or groups of species, used in the compilation of Figs 2-13 were obtained by taking into account correction factors as explained under 'Material and Methods'. (See Figs. 2-5).

When considering Fig. 2, it will be noticed that the visitation of *Onthophagus* spp. to Carcass B follows a fairly distinct pattern. Insect numbers reach a maximum at 20h00 of each day, with another much lesser peak at 08h00. Similar patterns can be found in many of the other figures depicting visitation patterns of individual species or groups of species. Where this underlying pattern is obscured by large irregular fluctuations within each 24-hour period, the insect numbers are given in histograms as totals per day (see Figs 8-12).

It is less easy to find a pattern when examining the numbers of insect species visiting Carcass B, as can be seen in Fig. 13. However, this is to be expected as the fluctuations exhibited in the numbers of insect individuals present at the carcass were caused by periods of extreme abundance or scarcity of only a few species. In general, therefore, the number of insect species present at Carcass B, per day, fluctuated only minimally throughout the study period.

No comparable figures were drawn for Carcass C as the low numbers of insect individuals and species did not lend themselves to such an exercise. Figure 13, illustrating the situation at Carcass B, was considered sufficient to indicate the general situation applicable to both carcasses.

No graphic representations or histograms are presented for species present only in very low numbers or which were present at the carcasses on very few occasions. This does not apply to the hymenopteran family Diapriidae, individuals of which were observed among pupae of *Chrysomya albiceps* under Carcass B. However, as was the case for ants, none of the collecting methods employed at the time proved effective for efficient collection. Rather than supply doubtful numerical results, their presence at Carcass B was recorded as present, common or abundant. (See Figs. 6-13).

Discussion on the immature stages of Chrysomya albiceps *and* Chrysomya marginalis

Arrival of adult female blow-flies occurred within an hour after placement of the carcasses and calliphorid eggs were first observed at 16h00 of Day 1, both at Carcasses B and C. The eggs were present as large masses in protected, concealed or shaded positions such as the axil regions and interface between soil and carcass.

The first emerged larvae were observed at 04h00 of Day 2 and by 08h00 thousands of these larvae were present at both carcasses on the edges of the abdominal incisions, in the mouths, nostrils and axil regions. From these regions the maggots migrated outwards, those in the axil regions achieving this in a distinct manner best

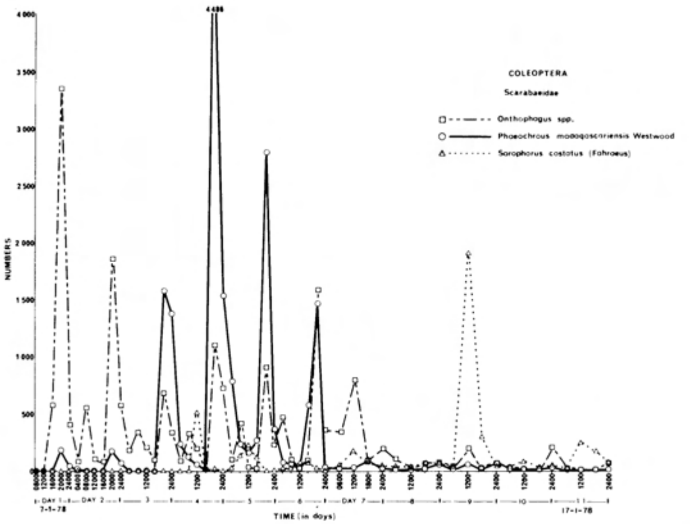

Fig. 2. Visitation patterns of *Onthophagus* spp., *Phaeochrous madagascariensis,* and *Sarophorus costatus* (all Scarabaeidae) to Impala Carcass B, Pafuri, January 1978. Within each 24 hour cycle, *Onthophagus* spp. reached maximum numbers at 20h00, a minimum at 04h00, with another lesser peak at 08h00. In general, *Onthophagus* spp. reached maximum abundance on Days 1 and 2, *P. madagascariensis* on Days 3 to 6, and *S. costatus* on Day 9.

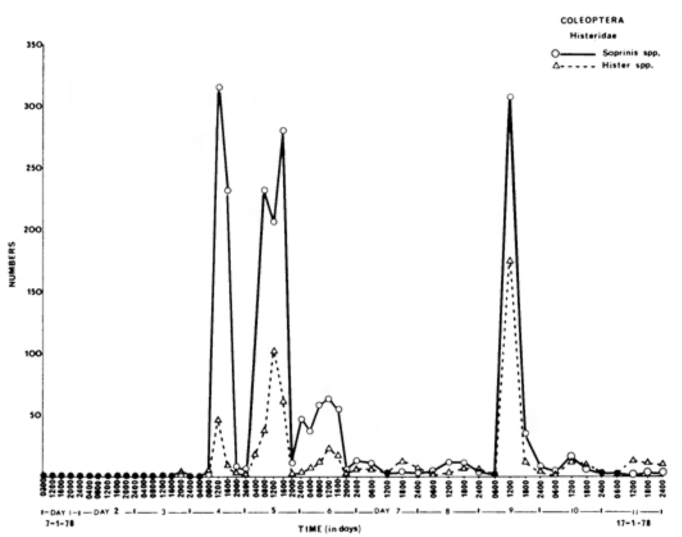

Fig. 3. Visitation patterns of *Saprinis* spp. and *Hister* spp. (Histeridae) to Impala Carcass B, Pafuri, January 1978. Both genera follow similar visitation curves, with maxima on Days 4 to 6, and Day 9. A distinct preference for daylight hours is also apparent.

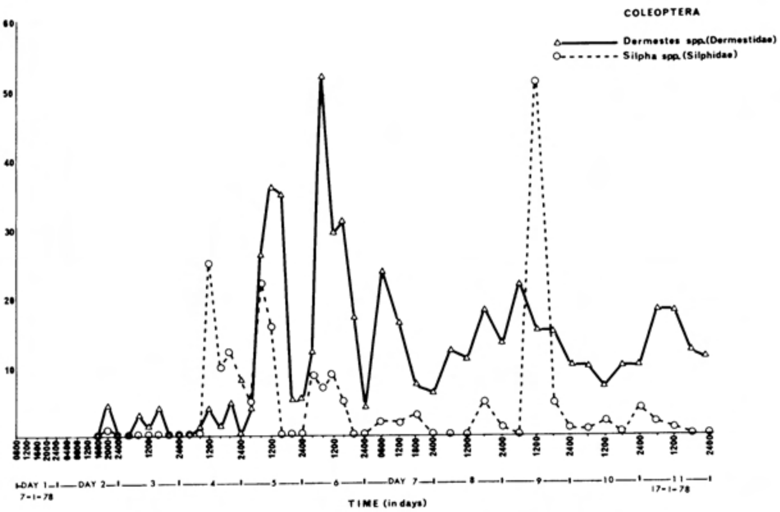

Fig. 4. Visitation patterns of *Dermestes* spp. (Dermestidae) and *Silpha* spp. (Silphidae) to Impala carcass B, Pafuri, January 1978.

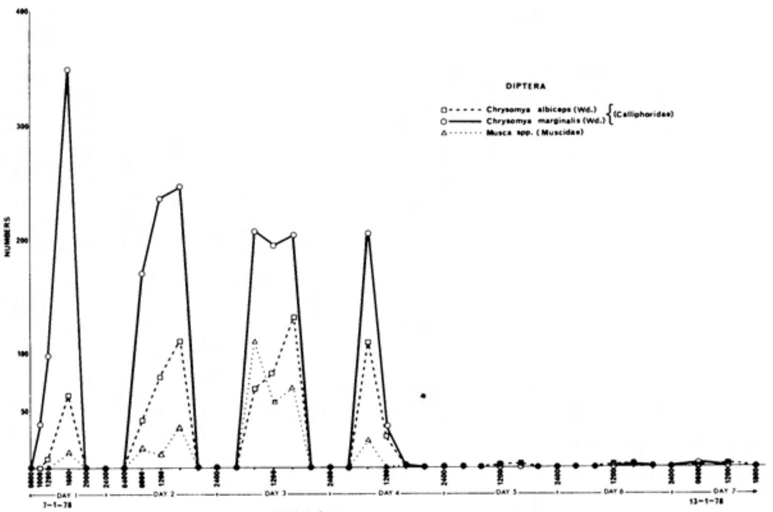

Fig. 5. Visitation patterns of *Chrysomya albiceps, Chrysomya marginalis* (Calliphoridae), and *Musca* spp. (Muscidae) to Impala Carcass C, Pafuri, January 1978. *C. marginalis* reaches maximum numbers on Day 1, decreasing steadily to Day 4, whilst hardly any are present from Day 5 onwards. Whilst numbers of *C. marginalis* decrease, those of *C. albiceps* increase steadily to Day 3, with a slight drop on Day 4. *Musca* spp. show a similar pattern to *C. albiceps*. Although not quite obvious from the graphs, there was a general maximum of these flies at 16h00 of each day, whilst a total absence of *Chrysomya* spp. and *Musca* spp. was observed at night.

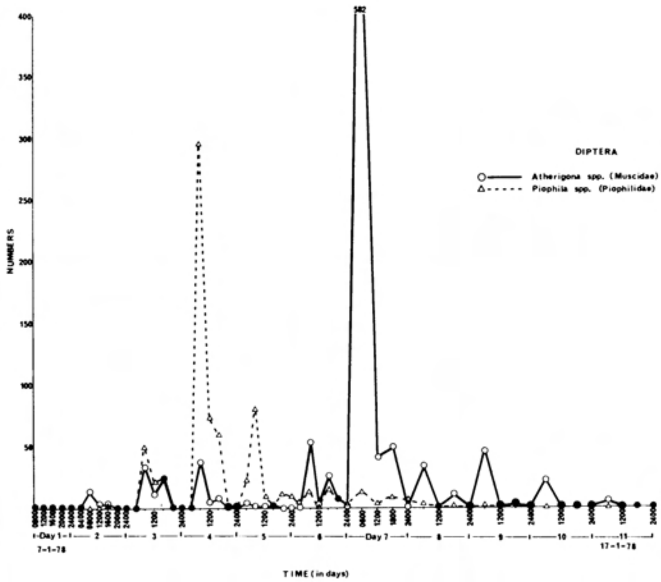

Fig. 6. Visitation patterns of *Atherigona* spp (Muscidae) and *Piophila* spp. (Piophilidae) to Impala Carcass C, Pafuri, January 1978. *Piophila* spp. have a period of abundance from Days 3 to 5, whilst *Atherigona* spp. reach maximum numbers on Day 7.

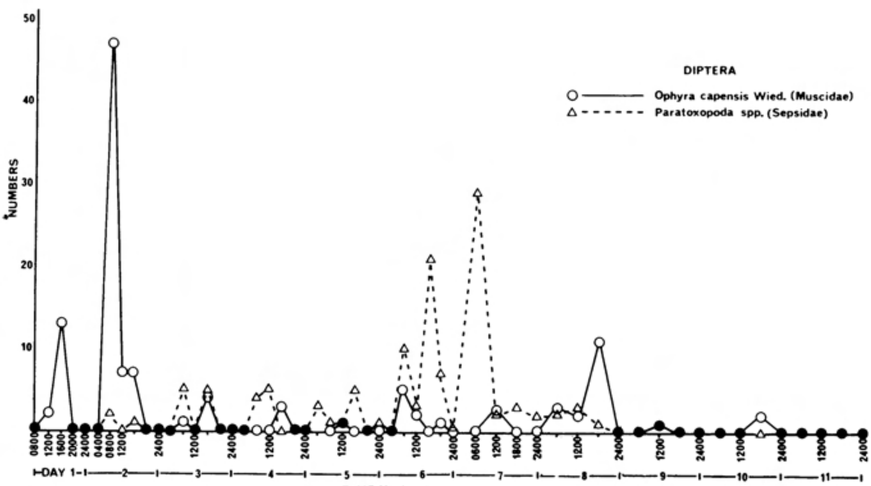

Fig. 7. Visitation patterns of *Ophyra capensis* (Muscidae) and *Parataxopoda* spp. (Sepsidae) to Impala Carcass C, Pafuri, January 1978. *Ophyra capensis* has a general abundance peak on Days 1 and 2, with that of *Paratoxopoda* spp. on Days 6 and 7.

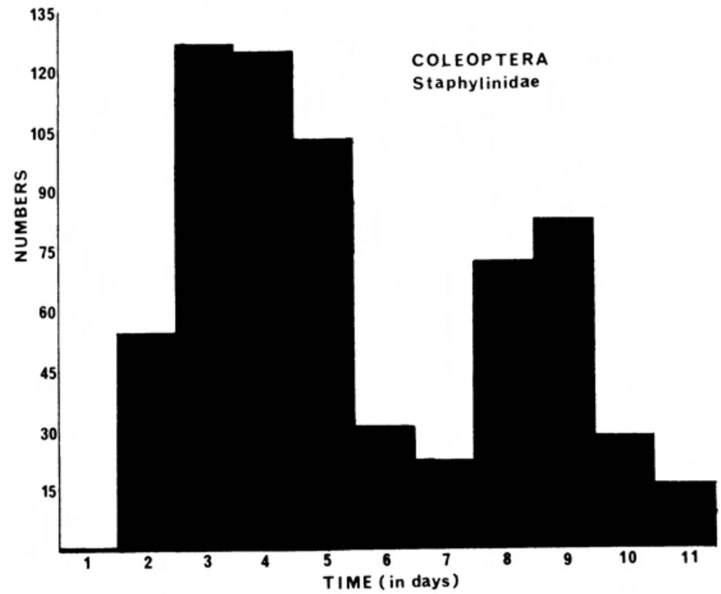

Fig. 8. Visitation pattern of Staphylinidae to Impala Carcass B, Pafuri, January 1978, given as daily totals.

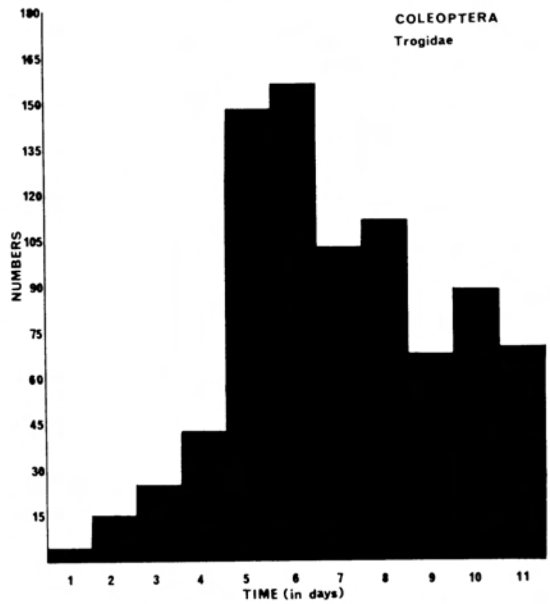

Fig. 9. Visitation pattern of *Trox* spp. (Trogidae) to Impala Carcass B, Pafuri, January 1978, given as daily totals. Maximum abundance is reached on Day 6, decreasing to Day 11.

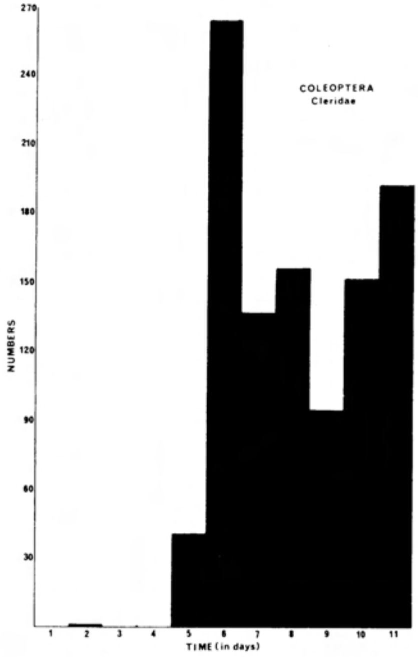

Fig. 10. Visitation pattern of Cleridae to Impala carcass B, Pafuri, January 1978, given as daily totals.

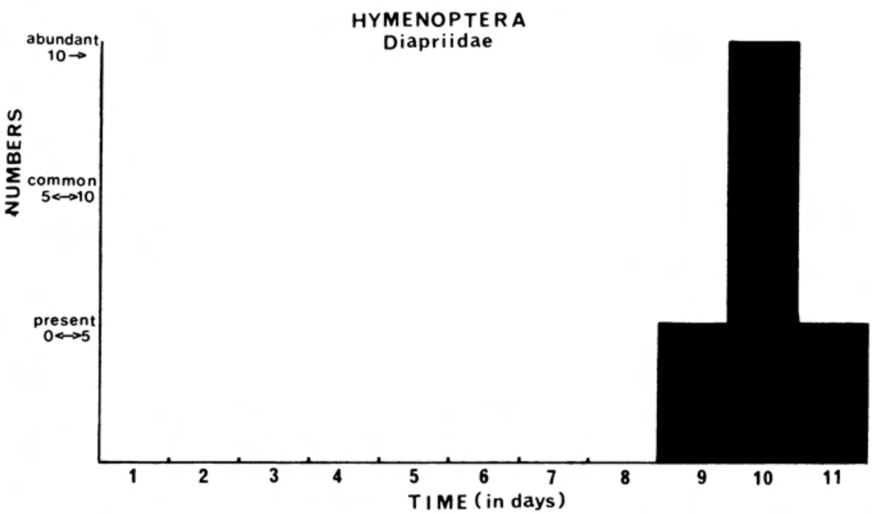

Fig. 11. Visitation pattern of Diapriidae to Impala Carcass B, Pafuri, January 1978, given as daily totals. Maximum abundance corresponds with the period when the most calliphorid pupae were present.

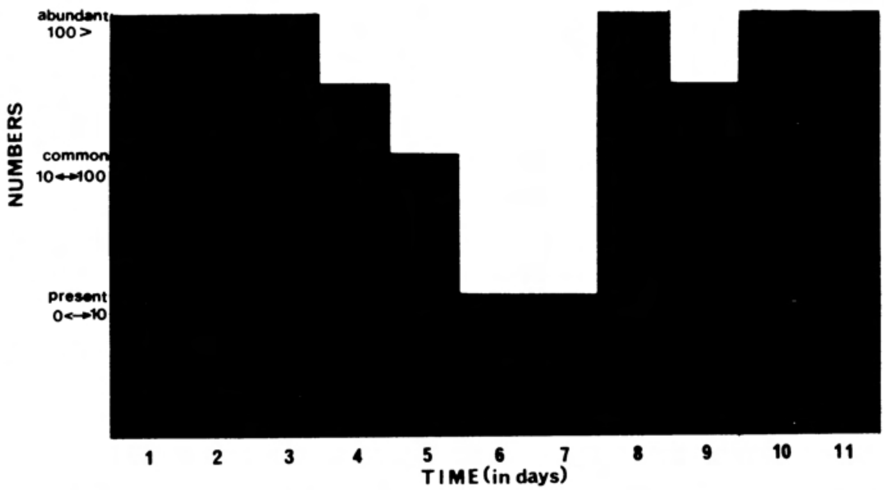

Fig. 12. Visitation pattern of Formicidae to Impala Carcass B, Pafuri, January 1978, given as daily totals. Two distinct abundance peaks are apparent, one lasting from Day 1-3, and another from Day 8-11.

described as 'subcutaneous streaming'. This refers to the situation where the larvae migrate in long finger-like extensions just beneath the skin. Feeding by larvae in this manner resulted in the skin being stripped of hair, this then deposited alongside the carcass.

The maggots increased in size at a tremendous rate such that by 12h00 of Day 3 *Chrysomya marginalis* larvae were ±1,2 cm in length, *C. albiceps* larvae being slightly shorter. *C. albiceps* larvae are very easily distinguishable from those of *C. marginalis* by their characteristic fleshy protuberances or "hairy" appearance.

By 12h00 of Day 4 a small number of maggots *(C. marginalis)* were leaving and attempting to burrow into the soil around both Carcasses B and C. At 08h00, Day 5, *Chrysomya marginalis* larvae were migrating away from Carcass C in a solid, thick stream. There had been no indication of this imminent migration at 04h00, and at 12h00 all that remained of this migrating mass were a few scattered groups of larvae attempting to burrow into the soil. This mass migration of *C. marginalis* larvae was also exhibited at Carcass B, but at 12h00, Day 6.

Larvae of *Chrysomya albiceps* lacked the conformity to an easily recognizable pattern. Many burrowed into the soil directly below the carcass, many refrained from digging in but pupated above the soil immediately next to and below the carcass and a small number crawled away from the carcass in all directions to pupate 1-3 m away. Furthermore there was no "synchronized" departure from the carcass; pupation being indicated rather by the gradual diminishing in larval numbers over a protracted period of about four days, commencing on Day 6.

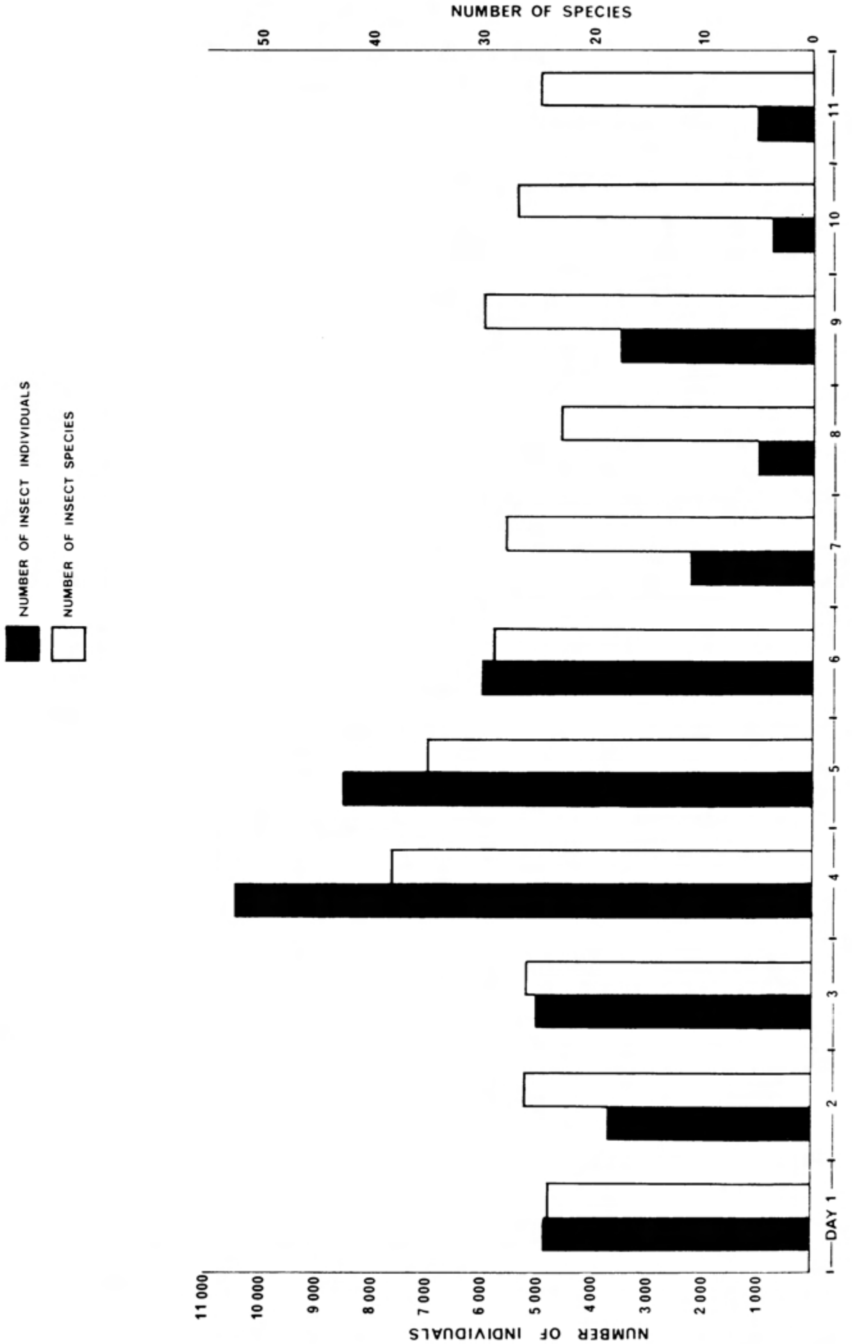

Fig. 13. Daily totals of insect individuals and insect species visiting Impala Carcass B, Pafuri, January, 1978, excluding Diapriidae, Formicidae (Hymenoptera) and all Diptera. Both insect numbers and species reach a maximum on Day 4.

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