THE LARGER INVERTEBRATE FAUNA OF THREE RABBIT CARCASSES

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(With 2 Figures in the Text)

During a university entomology course held at the Juniper Hall Field Centre, Dorking, in 1951, daily investigations were made for two weeks by a group of students* on the larger invertebrate fauna of three rabbit carcasses. In the evening of 4 July three freshly killed rabbits were put out in places separated by approximately 30 and 40 m. Carcass (A) was placed just inside a small shrubbery with no undergrowth and amongst partly rotted leaves. This habitat was generally dry and in deep shade. (B) was placed on cinders in loose sward under a large plane tree; this habitat was more subject to early morning dew than (A) and was exposed to light. (C) was situated in thick grass near the open verge of a meadow. Each carcass was covered with wire-netting pegged down at the corners to prevent disturbance by foxes and dogs. During examination this netting was removed and the carcass in each case was disturbed. Daily observations were made between 0800 and 0830 h G.M.T., 5–18 July inclusive. In many cases it was necessary to collect specimens for identification. In only a few instances did specimens escape unrecorded, and these represent only a fraction of the fauna present on examination. Not all specimens seen or caught have been fully identified, but specific determinations have been undertaken where possible. Grateful acknowledgement is made to the members of the staff of the Brit. Mus. (Nat. Hist.) who came to our aid with the more difficult species.

LIST OF SPECIES OBSERVED

Mollusca
- *Pomatias elegans* Mull. and other species.

Isopoda
- *Armadillidium* sp. and other species.

Arachnida
- Araneida
- Acarina

Insecta
- Dermaptera
  - *Forficula auricularia* L.

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INSECTA (*cont.*)
HEMIPTERA
Nabis lativentris Boh. and other species.
COLEOPTERA
Carabidae
Harpalus rufipes (Deg.)
Pterostichus niger
Hydrophilidae
Cercyon lateralis (Marsh.)
C. unipunctatus (L.)
Silphidae
Necrophorus humator (Goeze)
N. vespillo (L.)
Thanatophilus rugosus (L.)
T. sinuatus (F.)
Ptomophagus subvillosus (Goeze)
Catops fuscus (Pz.)
C. kirbii (Spence)
Staphylinidae
Oxytelus sculpturatus Gr.
Philonthus laminatus (Cr.)
P. fuscipennis (Man.)
Creophilus maxillosus (L.)
Tachinus rufipes (Deg.)
Aleochara curtula (Goeze)
Histeridae
Saprinus semistriatus (Scrib.)
Hister striola Sahl.
H. cadaverinus Hoff.
H. carbonarius Hoff.
Cantharidae
Metacantharis clypeata (Ill.)
HYMENOPTERA
Braconidae
Alysia manducator (Panz.)
Cynipidae
Figites laevigatus Dahl.
Formicidae
Myrmica laevinodis Nyl. and other species.
Vespidae
Vespula vulgaris (L.)
DIPTERA
Therevidae
Thereva sp.
Piophilidae
Piophila varipes Meigen
P. foveolata Meigen
Sphaeroceridae
Limosina luteilabris Rond.
Calliphoridae
Sarcophaga sp.
Calliphora sp.
Lucilia sericata (Meig.)
Muscidae
Hydrotaea armipes (Fallen)
Fannia scalaris (Fabr.) and other species.

Of previous work on the insect visitors to carrion, a large proportion was concerned with the blowfly problem in sheep-rearing areas of Australia and South Africa. Any attempt to obtain quantitative data on blowfly numbers was clearly beyond the scope of this work, but rough estimations of numbers of other insects were obtained without introducing too great a degree of artificiality into the observations. It was not found possible to collect and breed out the insects on the completion of the observations.

Fuller (1934) recognized three stages of decomposition of carcasses:

(1) In which the freshly killed host was not smelling strongly.

(2) Beginning when active liquefaction and disintegration became noticeable. Characterized by a strong smell and the frequency of dipterous larvae and Coleoptera.

(3) The drying of the carcass with loss of smell.

In the carcasses the onset of the second phase began in all cases on about the fourth day, with reduction of the numbers of larvae on A and C beginning on the 7th day. In both these cases the third, drying, phase was apparent by the 9th day. In the case of B, however, the second phase continued from the 4th until at least the 14th day.

Assuming that all the carcasses were equally accessible to the blowflies for egg laying, a reasonable assumption, having regard to the work of Gilmour, Waterhouse & McIntyre (1946), the causes of these major differences may be due either to differences in the associated insects or to the different effects of varying microclimatic conditions.

The proximity of the three carcasses to each other was such that there was no reason to assume that they were accessible to distinct faunas except in so far as these were affected by the microclimate.

The carcass A was in shade and thus protected to some extent from external moisture while, conversely, its position was such as to keep the temperature low and evaporation rate low. B was more exposed to the atmosphere and thus subject to wetting by dew and rain but also to higher temperature and a higher evaporation rate. Further, this carcass was on cinders so that the surface moisture was rapidly drained away from it. C was in long, damp grass and so was perpetually wet but at the same time in no way shaded from the sun. The high temperature and humidity conditions at C were, perhaps, optimal for decomposition, while those at A were similarly damp but rather cooler. B, on the other hand, was subject to drying in the daytime but the constant wetting by dew and rain kept the carcass in an available condition for fly larvae for much longer than was the case with the other two carcasses. Because of this extension of the second phase B was far more productive of insects than either of the other carcasses and most of the following observations refer to this carcass.

The insects visiting the carcasses fall into two groups: those scavenging on the carcass itself and those parasitic or predaceous on the dipterous larvae. By far the most important scavengers were the dipterous larvae themselves. Adult Diptera were observed at all the carcasses on the 1st day and larvae were first seen on the 3rd, 4th and 5th days on B, C and A respectively. A drop in numbers of larvae in A and C was noted after the 6th day. This possibly resulted from the intense competition between the larvae, and as such the drop resembled that figured by Holdaway (1930), but was no doubt also due to some numbers of the larvae leaving the carcass to pupate, since the larvae of *Lucilia sericata* mature in about three days from hatching (Ullyett 1950) and migrate away from the carcass to pupate.

Other scavengers included the Diptera *Piophila* spp. and *Fannia scalaris* with scavenging larvae. Fuller (1934) and Myers (1929) regard *Piophila casei* (L.) as a late arrival, but in the present case *P. varipes* was seen on the 3rd day and Duffield (1937) records this and three other species of *Piophila* from carcasses stated to be 4 days old. Illingworth (1927) first records *P. casei* on the 3rd day of an experiment but it was most frequent after 6 days. From the description given it appears that by this time the second phase of decomposition was giving way to the third so that the carcasses were in an advanced state of decomposition. This brings out the importance of describing the state of decomposition, even if only using such simple criteria as smell and frequency of dipterous larvae, in addition to the age of the carcass. Clearly under different conditions of climate and accessibility the rates of decomposition will vary considerably so that the age of a carcass is not of great significance.

Additional scavengers were the ants and wasps, although the wasps might equally well have been predaceous on the fly larvae. The beetles of the families Silphidae and Histeridae may also have been either scavengers or predators, but opinions are divided as to their effects on the fly population. Holdaway (1930) regards the Histerids as important in the reduction in numbers of blowflies but, according to Salt (1932) the only factor of any importance in this respect is competition between the blowfly larvae themselves. Fuller sums the matter up adequately as follows, '...it is the

surplus of maggots, forced off the carcass before completing their development, which is seized and destroyed by the waiting predators. This surplus would otherwise have succumbed through starvation; consequently the beetles play no part in regulating the blowfly population.'

The commonest Histerid found during the observations was *Saprinus semistriatus* which did not appear at corpse B until the 4th day (Table 1 and Fig. 1). The numbers of this beetle remained relatively constant from the 6th day onwards except for a drop on the 9th and 10th days which were quite cold. This beetle was feeding on the dipterous larvae and this is correlated with its non-appearance until the latter were well established and also with its later constancy in numbers.

Table 1. *Summary of the more prominent insects visiting carcass B*

Arranged in families in order of appearance. Dipterous ova and larvae are indicated as present or absent.

	Day													
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Coleoptera														
Aleochara curtula	–	–	10	10	35	45	55	50	25	15	12	10	1	1
Necrophorus vespillo	–	–	–	1	1	–	–	–	–	–	–	–	–	–
Pterostichus niger	–	–	–	1	–	–	1	–	–	–	–	–	–	–
Saprinus semistriatus	–	–	–	1	6	19	20	20	15	5	20	20	15	18
Necrophorus humator	–	–	–	–	1	–	4	–	–	–	–	–	–	–
Hister cadaverinus	–	–	–	–	1	–	–	8	1	5	3	–	–	5
Creophillus maxillosus	–	–	–	–	–	–	2	2	–	1	3	1	–	5
Hister striola	–	–	–	–	–	–	–	1	1	–	1	1	2	1
Ptomophagus subvillosus	–	–	–	–	–	–	–	1	–	–	–	–	1	1
Thanatophilus sinuatus	–	–	–	–	–	–	–	–	1	2	1	1	–	–
T. rugosus	–	–	–	–	–	–	–	–	–	1	1	–	–	2
Philonthus laminatus	–	–	–	–	–	–	–	–	–	1	1	–	–	–
Hymenoptera														
Alysia manducator	–	–	–	2	5	5	–	5	–	–	–	–	–	–
Figites laevigatus	–	–	–	–	–	–	–	–	–	3	–	–	5	5
Vespula vulgaris	–	–	–	–	–	–	–	–	–	–	–	1	1	1
Diptera														
Calliphora sp.	5	2	5	–	–	–	–	–	–	–	–	–	–	–
Lucilia sericata	–	–	5	10	4	–	1	5	–	5	5	20	15	5
Sarcophaga sp.	–	–	–	10	4	–	1	10	5	5	5	–	–	5
Fannia scalaris	–	–	–	–	–	–	12	10	–	5	5	5	5	5
Ova	–	–	+	+	+	–	–	–	–	–	–	–	–	–
Larvae	–	–	+	+	+	+	–	+	+	+	–	+	+	+

The only undoubted scavengers among the Coleoptera were the *Cercyon* spp. and possibly some of the Staphylinids. The commonest Staphylinids were *Creophilus maxillosus* and *Aleochara curtula*, the latter being the most abundant beetle of all. *Creophilus maxillosus* is predatory in both larval and adult stages while *Aleochara curtula* is an obligate parasite of dipterous pupae and the adults feed on the fly larvae. *A. curtula* first appeared on the 3rd day (Fig. 1). Numbers rapidly increased until a maximum was reached on the 7th day after which they fell off equally rapidly. Wadsworth (1915) states that the adults of *A. bilineata* copulate within three days and then burrow in the ground. It appears that this is also true of *A. curtula*, the marked decline in numbers noted on the 9th day being four days after its arrival in any

numbers. The numbers of *A. curtula* recorded were considerable and, acting at a time when many hazards are past for the dipterous larvae, may well be of some importance in the reduction of blowflies.

The burying beetles, *Necrophorus* spp., first appeared on the 4th day and were last seen on the 7th. They made no progress in burying the carcass because of the disturbances caused by the daily observations. Walsh (1931) and Kaufmann (1941) give

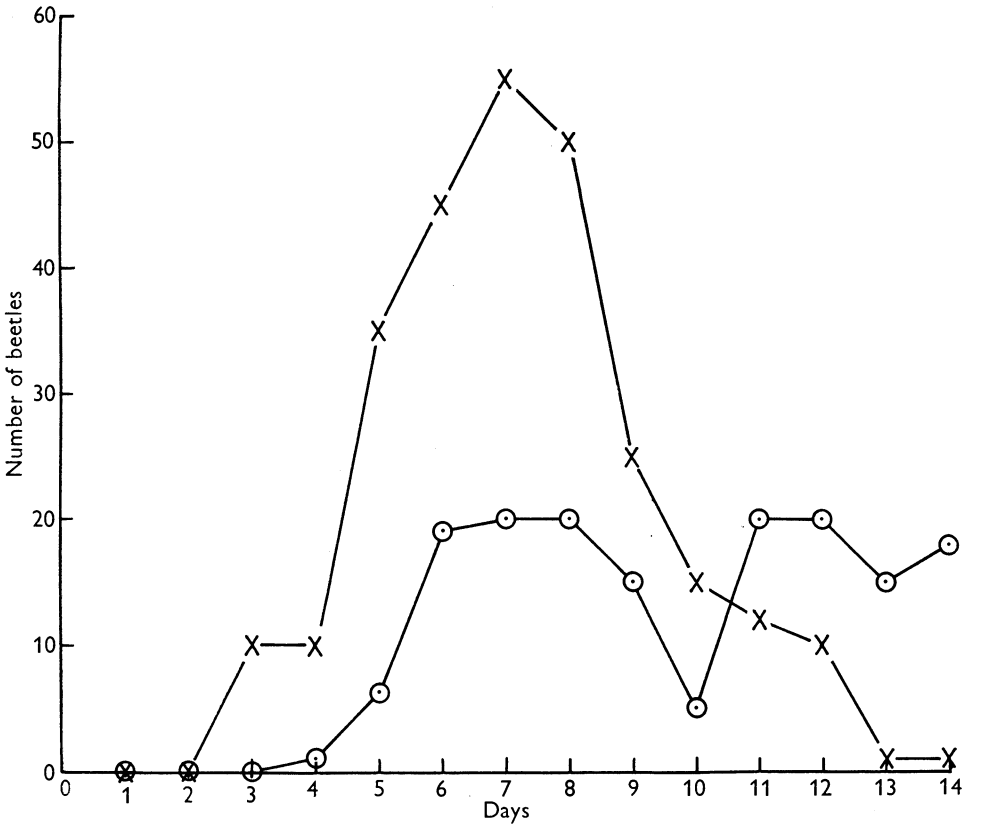

Fig. 1. Numbers of *Aleochara curtula* and *Saprinus semistriatus* visiting carcass B during the observations. ×, *Aleochara*; ⊙, *Saprinus*.

records of *N. humator* up to the end of October, but some of the specimens found during these observations were very heavily infested with mites, suggesting that they were approaching the end of their season (Fabre 1919).

The fly, *Hydrotaea armipes*, was first recorded on the 8th day. Its larvae probably lived at the expense of the blowfly larvae, and it would seem that *Hydrotaea* in Britain occupies the niche filled by *Chrysomyia* elsewhere. Both genera arrive late at the carcass and have predatory larvae with tough spiny skins.

Alysia manducator, a Braconid parasite of dipterous larvae, was first observed on day 4 at carcass B and on day 5 at carcass C. No more than five specimens were seen at any one time, and it is doubtful if the degree of infestation was high. Graham-Smith (1919) has shown that the degree of parasitism is much higher in the autumn than in

the summer. Salt (1932) regards *A. manducator* as an effective parasite since, because of the habit of ovipositing in half to full-grown larvae (Altson 1920), it attacks the dipterous larvae after the effects of overblowing have become apparent. This contrasts with the Cynipid, *Figites laevigatus*, which was first recorded on day 10. This species oviposits only in first- and second-instar larvae and shows a preference for hatchlings (James 1928) with the result that a number of larvae are parasitized which would have died in any case due to their inter-specific competition.

The whole succession may be drawn together by constructing a food chain (Fig. 2). In this the division into scavengers and predators becomes evident, and it can be seen that, apart from the dipterous larvae, no great numbers of scavengers were involved, almost all the other insects being predators or parasites of the larvae.

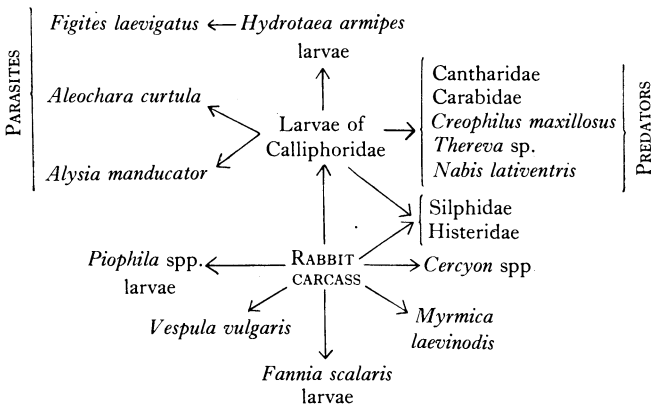

Fig. 2.

Some attempt has been made to correlate the frequency of visiting adult insects with the weather conditions (Table 2). The weather data were taken from the station in the grounds daily at 0900 h G.M.T. The rainfall figures refer to the previous 24 h.

The total number of insects increased over the first five days, this being connected with the stage of decomposition. On the 5th day Coleoptera and Hymenoptera first appeared in numbers and altogether 113 insects were counted. Days 6 and 7 were dull and the numbers of insects observed decreased, although air temperature remained high. Numbers rose sharply on the 8th day, which was warm and sunny, but fell again next day which, despite the presence of sun, was cold and very wet. On this day there was a large reduction in the numbers of beetles present, but this was probably associated with the maturation of the *Aleochara* rather than with the weather. Day 10 continued cold but less wet, with an increase in the numbers of adult Diptera. The fly larvae were not apparent from the outside on day 10, although they were seen in some numbers on subsequent days. It is probable that on day 10 they took refuge within and below the carcass to avoid the low temperatures. After this the numbers of insects observed rose again as the weather improved and temperatures went up, but the numbers recorded were never as high as those obtained previously. This was probably due to the fact that the corpses were now losing their attraction for many of the insects.

The dipterous larvae were the only scavengers of any consequence in the decomposition of the carcasses. They provided the basis on which the rest of the fauna, consisting mainly of predaceous beetles and parasitic Hymenoptera, depended. In two of the carcasses described here three stages of decomposition were observed, but in the third carcass the second stage was greatly prolonged, no drying of the corpse

Table 2. *Summary of weather conditions and adult insects visiting the carcasses during the observations*

For purposes of tabulation the weather is described as: sunny—clear sky, bright sun; cloudy—bright day, sun obscured by cloud; dull—heavy, overcast day.

Date (July)	Day	Temp. (° C)	Rainfall (mm)	Weather	Insects				
					Diptera	Hymen-optera	Cole-optera	Other orders	Total
5	1	18·5	0	Sunny	15	10	1	11	39
6	2	19·7	0·7	Sunny	14	—	2	5	21
7	3	19·1	0, heavy dew	Dull	38	5	10	—	53
8	4	19·5	0	Cloudy	31	2	22	—	55
9	5	19·8	0	Sunny	26	25	62	—	113
10	6	19·7	3·4	Dull	—	5	68	5	78
11	7	20·0	0	Dull	36	—	48	5	± 84
12	8	19·7	2·0	Sunny	33	1	84	10	138
13	9	17·7	10·0	Sunny	5	—	38	1	44
14	10	17·5	0·3	Dull	20	1	29	—	50
15	11	18·7	0	Sunny	30	20	21	21	92
16	12	19·3	0	Sunny	25	1	34	—	60
17	13	20·0	0	Sunny	20	6	36	5	67
18	14	21·0	0	Sunny	45	6	32	—	83
Total insects visiting the carcasses					339	82	487	63	

occurring before the end of the observations. The most abundant beetles were the Staphylinid *Aleochara curtula* and the Histerid *Saprinus semistriatus*. Numbers of adult insects varied from day to day with the weather conditions but showed an overall increase during the first eight days, followed by a decrease over the next six, this being correlated with the state of decomposition of the carcasses.

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