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Abstract

Arthropods associated with cricket carcasses placed on top and within deciduous forest litter were collected over a 12 month interval. Vespid wasps and ants quickly removed carcasses left on top of forest litter, but carcasses placed within litter persisted throughout the study. Major consumers of carcasses in litter varied seasonally; maggots dominated on fresh carcasses in summer, but fresh carcasses placed in litter in autumn were consumed by other arthropods. A gamasid mite, Hypoaspis (Laelaspis) johnieae dominated the microarthropod fauna found on exoskeleton fragments. A method for collecting invertebrate carrion feeders and measuring carrion disappearance is presented.

Introduction

Vertebrate decomposition and the organisms responsible for the consumption of vertebrate carrion are well known (e.g. Paine 1965; Cornaby 1974; Johnson 1975; Putman 1978). In contrast, few data are available on invertebrate decomposition or the organisms involved in invertebrate carrion consumption. Nonpredatory mortality of invertebrates is seldom observed or considered in bioenergetic studies. However, mortality due to disease or other nonpredatory factors may be considerable in certain arthropod groups (e.g. White et al. 1979). Arthropod exoskeleton remains are commonly observed in sections of forest litter and soil (Anderson 1978; Seastedt et al. 1980). Do arthropod remains provide an energy and nutrient source for a specialized arthropod fauna? We measured the rate of disappearance of arthropod carrion and collected arthropods associated with these remains. A method suitable for collecting carrion feeders and measuring carcass disappearance rates is presented.

Methods

The study site was located in an oak-hickory forest at the University of Georgia Botanical Gardens near Athens, Georgia, in the piedmont region of the Southeastern United States. The region has a mild moist climate with winter temperatures seldom remaining below freezing (January mean temperature = 6.3 C; NOAA data). Rainfall averages approximately 130 cm per year, and precipitation is fairly evenly distributed over the year. The immediate study area has been the site of several ecological investigations, and descriptions of the study site are provided by Chittin (1977) and Best et al. (1978).

Domestic crickets, Acheta domesticus (L.), were obtained from a local supplier of fish bait, killed by freezing, individually weighed and stored in a freezer until placed in the field. The litter bag method of Crossley and Hoglund (1962) was selected as a means of containing and retrieving cricket carcasses. Crickets were placed individually in small (5 cm^2) nylon mesh bags with openings of approximately 2 mm^2 . Fifty of these bags were placed in the litter at one time, and a small sample (usually 4) were harvested at 2 to 4 day intervals for the first 10 days. Bags were harvested at more widely separated intervals thereafter. Large arthropods found on carcasses were removed by hand, and the cricket remains were then placed in Tullgren funnels to remove microarthropods. Remains were dried at 60C and weighed. Initial dry weights of crickets were estimated from a regression equation calculated from wet and dry weights of a sample of 20 crickets.

The effects of litterbag containment and location of the carcasses with respect to disappearance rates were assessed. Thirty crickets were

placed on top of the forest litter after first attaching threads around each individual. Markers were attached to the threads as a means of relocating the carcasses. Crickets in litter bags were placed adjacent to tethered carcasses. A second set of tethered and bagged carcasses were placed in the fermentation zone (F-layer) of the forest litter. A wire mesh cover (ca. 2 cm mesh) was placed over these carcasses prior to replacing litter. It was therefore possible to examine crickets without excessive disturbance to the carcasses themselves.

The first set of carcasses was placed in the field in July 1978, and all were harvested by late August. A second experiment, consisting of 100 bagged samples, was initiated in the fermentation zone of the litter in October 1978. We attempted to measure the percentage of arthropods present in the bags at the time of sampling that were not feeding on cricket remains or preying upon those organisms attracted to the carcasses. In addition to carcasses, 40 bags containing plastic vial caps were also placed in the litter. These caps had approximately the same surface area as the crickets. Their serrated edges and construction provided substrate for microarthropods, but the plastic had no nutritional value. By comparing numbers and species composition of microarthropods found on carcasses and vial caps, the attractiveness of carcasses as a food resource could be assessed.

Results

Carcasses on Top of Forest Litter

Vespid wasps discovered the tethered and bagged cricket carcasses within minutes of their placement on top of the forest litter. A few of these wasps were captured and identified as Vespa squamosa (Drury), though other species may have been present. The wasps dismembered the crickets and flew off with large pieces. The nylon litter bags did not protect the carcasses; wasps chewed through the mesh and removed the

crickets. Ants also gathered at the remains and may have obtained a few pieces. Observations were not made continuously: thus, the importance of ants as surface carrion feeders was likely underestimated. Within 24 hours, however, all tethered and bagged carcasses had disappeared.

Carcasses in Forest Litter

Both tethered and bagged carcasses in litter disappeared much more slowly than those left on top of the litter. Tethered carcasses were quickly dismembered and spread over the forest floor. However, cricket remains (mostly wings, legs and pronota) were observed after three months in the field. Organisms feeding on tethered carcasses were not collected; however, ants and beetles appeared to be responsible for most of the consumption.

Litter bags buried in litter did not prevent larger invertebrates from obtaining carrion. Large holes were evident in some of the bags, and several litter bags disappeared entirely. Large parajulid millipedes, snails and ants were occasionally found on the outside of the bags, and these organisms were probably feeding on the carcasses. Arthropods found inside the bags placed in the field in summer are reported in Table 1. In terms of numbers and biomass, maggots (phorids, sarcophagids, and perhaps others) dominated during the first week of the summer study. Some of these maggots removed from bags were placed in containers without food and successfully pupated and emerged as adults. Thus, cricket carrion provided sufficient food and substrate for complete development of these insects. The decomposition process of the bagged crickets was similar to that described for vertebrate carcasses (e.g. Johnson, 1975). Crickets passed through an anaerobic "bloat" stage, followed by a period of rapid decay, followed by a dry stage. Unlike

vertebrate carrion; however, this process could be interrupted by total or near total consumption by ants, beetles or other macroinvertebrates. The time involved for a carcass to be reduced to exoskeleton fragments was about a week to 10 days.

Mesostigmatid (gamasid) mites were the most abundant group of microarthropods on carcasses during the summer experiment (Table 1). Hypoaspis (Laelaspis) johnieae (Hunter and Glover) composed over half of the gamasid mites. The trophic status of this mite is uncertain; however, its abundance suggested that these mites fed on liquids from the decomposing carcasses. This species may also have been feeding on other groups attracted to the carrion. Other abundant groups found on carcasses consisted of Collembola (mostly entomobriids and hypogasturids) and an unidentified species of anoetid mite. Many collembolans are generalist feeders, and typically fungivorous or phytophagous species have been reported to feed on invertebrate remains (Maynard, 1951). Anoetids are rare in forest litter and soil, but are common in damp, decomposing plant material (Krantz, 1978). Interestingly enough, numbers of microarthropods peaked on cricket remains on the last collection date, when only about 10% of the initial weight of the crickets remained. Some indication that the food source was becoming limited at this time was the observation that over 80 percent of the anoetid mites collected from 26 day-old carcasses were nonfeeding forms (hypopi).

A very different pattern of arthropod composition was observed on carcasses placed in litter in October. That month was unusually dry and carcasses appeared to mummify rather than decay as in the summer experiment. Only two maggots were recovered from the carcasses, and the numbers of arthropods found on the carcasses were

reduced (Table 2). Unlike the summer experiment, anoetid mites (Astigmata) were absent during the first month and hypoaspid mites, while present, were much reduced in numbers when compared to the summer experiment. Hypoaspis johnieae appeared to be the only species uniquely attracted to the carrion. Only a single specimen of this species was found on the 40 bags containing plastic caps. The carrion bags contained an average of about twice as many arthropods as did bags containing plastic caps (Table 2), and the difference in microarthropod numbers found on these two substrates was significantly different (Wilcoxin Sign Text, $p < .05$). Only one specimen of H. johnieae was found on carcasses after the first month of the autumn experiment. By mid-November and thereafter, the composition of the fauna on carcasses resembled that found on the non-nutritive substrate. Moreover, the relative dominance of oribatids, prostigmatids, mesostigmatid mites and collembolans was similar to that observed for litter samples obtained from the Botanical Gardens (Merchant and Crossley, 1970). Thus, while microarthropods were attracted to exoskeleton remains, the fauna using this resource resembled that found in decomposing leaf litter.

Weight loss by cricket carrion was much greater during the summer experiment; only about 10% of the original weight remained after 26 days in litter during summer, while about 30% remained after this time in autumn (Tables 1 & 2). The difference was attributed to the reduced numbers of arthropods feeding on the carrion, and particularly to the reduced numbers of maggots. Somewhat surprisingly,

approximately 17% of the initial dry weight of the carcasses remained within bags after a full year in forest litter. A portion of this weight must be attributed to fungal hyphae and debris that became associated with exoskeleton fragments. However, after the first few weeks in litter, the cricket remains were not heavily used as an arthropod food source.

Discussion

The numbers and composition of the arthropod community found on cricket carcasses appear to be a function of (1) the location of the carrion, (2) the age of the carcass and (3) the microclimatic regime surrounding the carcass. Arthropods dying on the litter surface are quickly removed by wasps or ants. Whether these social insects completely consume the carcasses or deposit exoskeleton remains elsewhere was not determined. The disappearance of invertebrate carrion in litter is a stochastic process. Carcasses may be entirely consumed by macroinvertebrates, or partially consumed by a variety of different invertebrate species. Overall, however, maggots, ants and beetles appear to obtain much of the biomass. Fragments that escape macroinvertebrate consumption are colonized by a variety of microarthropods, and at least one species, Hypoaspis johnieae, appears to specialize on these remains. Many, if not most, collembolans and oribatid mites contain a gut flora capable of digesting chitin (Maynard, 1951; Luxton, 1972), and these organisms are likely responsible for the eventual disappearance of exoskeleton fragments. Older exoskeleton fragments are usually infused with fungal hyphae (Seastedt et al. 1980). Microbial breakdown of these

may be the primary agent of exoskeleton decomposition while microarthropods perform an auxilliary function by fragmenting exoskeleton materials and grazing upon both arthropod remains and microflora.

Data presented in Tables 1 and 2 include arthropod taxa which remain in bags for a portion or much of their life cycles (e.g. maggots, many microarthropods), and taxa feeding or collecting fragments but residing elsewhere (e.g. ants, beetles). The litter bag method likely underestimated the importance of the more mobile carrion feeders. Collections of arthropods by periodic sampling is biased in favor of those organisms that feed in situ, and the method is most likely to collect those organisms that remain in bags between feeding intervals. Thus, the data collected here were insufficient to quantify the transfer of carrion mass to carrion feeders. Future studies should employ more frequent sampling during the early stages of decomposition or use the pitfall method of Putman (1978) to quantify energy transfers from carrion or to collect an adequate sample of the larger, more mobile species attracted to invertebrate carrion.

Results from this study suggest that species previously considered vertebrate carrion feeders may also feed on invertebrate carrion. A different species of one of the genera of beetles found on cricket carcasses, Onthophagus, has been reported to feed on vertebrate carrion (Cornaby, 1974). Dipteran species can complete development on cricket carcasses, as observed in this study, or on cicada carcasses (White et al., 1979). Whether these same dipteran species also use vertebrate

carriion is unknown; however, as the influx of both vertebrate and invertebrate carrion to the forest floor is likely a rare event in space and time, certain carrion feeders may opportunistically exploit either resource.

Arthropod exoskeleton fragments are produced not only as a result of nonpredatory mortality, but also from arthropod molts and as 'orts' or 'rejecta' from arthropod predators and parasitoids. The amount of this material in forest litter and soil is relatively large. Cornaby (1973) estimated an average standing crop of about $1 \text{ g} \cdot \text{m}^{-2}$ of arthropod exoskeleton material in litter and humus from a southeastern U.S. pine forest compared with a standing crop of about $1.2 \text{ g} \cdot \text{m}^{-2}$ of living arthropod biomass. However, with the exception of Hypoaspis johnieae, this potential food resource does not appear to support a unique arthropod fauna. Instead, exoskeleton fragments appear to decompose slowly as a result of microbial and microfaunal interactions similar to those responsible for leaf litter decomposition.

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Table 1. Density of Arthropods (number/bag), Summer 1978¹

ARTHIPOD TAXA	AGE OF CARCASS (DAYS)							Average
	2	4	6	8	12	16	26	
Insecta								
Formicidae	0.25	0	0.25	0	0.25	0	0	0.11
Scarabaeidae								
<i>Onthophagus striatulus</i>	0.25	0	0	0	0	0	0	0.04
<i>Glaphyrocantion virdis</i>	0	0.50	0.75	0	0	0	0	0.18
Hydrophilidae (Sphaeridiinae)	0	0	0.25	0	0	0	0	0.04
Unidentified larvae	0	0.50	1.00	0.50	0	0	0.50	0.36
Psocidae	0.50	0.50	0	0.75	0.25	0.75	0.25	0.43
Diptera, maggots	0	17.75	29.75	0.89	0	0	0	7.60
Collembola	1.25	0.25	0.75	1.25	16.75	9.00	3.50	4.68
Acarina								
Astigmata (Acaridida)								
Acaridae	0	0	0	0	0.50	0.25	0.75	0.25
Anoetidae	0	0.75	1.25	2.50	1.75	4.00	15.75	4.21
Prostigmata (Acetinedida)	0.75	0.25	0.25	0.50	0.75	1.00	0.75	0.61
Cryptostigmata (Oribatida)	2.00	1.00	1.00	0.75	5.75	4.50	6.25	3.04
Mesostigmata (Gamasida) Total	3.50	3.00	4.00	7.00	12.00	7.75	16.75	7.71
<i>Hypoaspis (Laelaspis)</i>								
johnieae adults	1.00	0.75	3.00	4.00	3.50	3.00	4.00	2.75
Other adults	0	1.50	0.50	0.50	2.75	1.00	3.00	1.32
Immatures (total)	2.50	0.75	0.50	2.50	5.75	3.75	9.75	3.64
Araneida	0.25	0	0	0	0	0.25	0.25	0.11
Others ²	0	0	0	0	0	0	0.75	0.11
TOTAL	8.75	24.50	39.75	19.50	38.00	31.50	4.53	29.54
AVERAGE CARCASS WEIGHT (% OF INITIAL WEIGHT)	67.3	46.6	27.6	13.9	11.7	11.2	9.5	

1. Average of four carcasses per date.

2. Symphylan, centipede and pseudoscorpion.

Table 2. Density of Microarthropods (number/bag), 1 October 1978 - 30 September 1979¹

Arthropod Taxa	Substrate ²	Age of Substrate (Days)													Average
		4	8	12	16	20	24	28	32	44	84	200	240	365	
Insecta															
Formicidae	C	0.75	0	0.25	0	0	0	0	0	0	0	0	0	0	0.08
	P	0.25	0	0	0	0	0	0	0	0	*	*	0	*	0.03
Coleoptera (larvae)	C	0	0	0.50	0.50	0.25	0.75	0	0.75	0	0	0	0	0.25	0.23
	P	0	0	0	0	0	0	0	0	0	*	*	0	*	0
Psocidae	C	0	0	0	0	0	0	0	0	0	0	0	0	0.25	0.02
	P	0.75	0	0	0	0	0	0	0	0	*	*	0	*	0.08
Diptera	C	0.75	0	0	0	0	0	0	0	0	0	0	0	0	0.06
	P	0	0	0	0	0	0	0	0	0	*	*	0	*	0
Collembola	C	0.75	0.25	0	0.75	0.75	0	0	0	0.25	1.00	1.50	1.25	0.75	0.56
	P	0	0	0	0	0.25	0.25	0	0	0	*	*	2.50	*	0.30
Acarina															
Astigmata	C	0	0	0	0	0	0	0	0	0.25	0	0	1.50	0	0.13
	P	0	0	0	0	0.25	0	0.25	0	0	*	*	0	*	0.05
Prostigmata	C	0	1.25	2.25	0.25	2.50	2.75	1.75	1.50	0.25	0.25	0.25	0.75	0.50	1.10
	P	0.75	0	0	0	1.00	0.25	0.25	0.50	0	*	*	1.50	*	0.43
Mesostigmata (total)	C	0.75	1.25	0.50	4.50	2.25	0	0.25	0	0	0.75	0.25	3.50	0.75	1.13
	P	0.50	0.25	0.25	0.50	1.50	0.50	0.50	0	0	*	*	3.75	*	0.55

Table 2, Continued.

Arthropod Taxa	Substrate ²	Age of Substrate (Days)													
		4	8	12	16	20	24	28	32	44	81	200	240	365	Average
<u>Hypobaspidis johniae</u>	C	0.75	1.25	0.25	3.50	1.00	0	0	0	0	0	0	0	0.25	0.54
	P	0	0	0	0	0	0	0	0	0	*	*	0.25	*	0.03
Cryptostigmata	C	1.00	1.25	1.75	2.50	4.00	2.25	0.75	0	1.50	1.00	1.00	12.75	3.50	2.56
	P	0.25	0	0	0.50	0.50	0	0.25	0.25	0.50	*	*	6.00	*	0.83
Araneida	C	0	0	0	0	0	0	0	0.25	0	0	0	0	0	0.02
	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other ³	C	0.50	0	0	0	0.25	0	0	0	0	0.25	0	0	0.25	0.10
	P	0	0	0	0	0.50	0	0	0	0	*	*	0	*	0.05
Total	C	4.50	4.00	5.25	8.50	10.00	5.75	2.75	2.50	2.25	3.25	3.00	19.75	6.25	5.98
	P	2.50	0.25	0.25	1.00	4.00	1.00	1.25	0.75	0.50	*	*	13.75	*	2.53
Average Carcass Weight (% of Initial Weight)		39.2	35.9	34.1	38.7	19.9	26.7	31.2	37.9	16.0	20.8	18.8	18.0	17.0	

1. Average of 4 crickets or plastic caps per date.

2. C = Cricket Carcass, P = Plastic Cap.

3. 2 wood roaches, 2 pseudoscorpions, 2 thrips, 1 proturan.

* No data.