

Population Ecology of Carnivores Associated with Carrion in Caves of Georgia, USA¹

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J. Entomol. Sci. 36(3): 305-311 (July 2001)

Abstract The abundance of troglomorphic *Megaselia* spp. (Diptera: Phoridae), troglomorphic *Calliphora vicina* Robineau-Desvoidy (Diptera: Calliphoridae), and troglomorphic *Ptomaphagus whitei* Barr (Coleoptera: Leiodidae) on carrion was studied in two caves in Georgia, USA. Phorid and leiodid abundance were statistically independent of location in the caves and of time the carrion was available for colonization in a cave. Calliphorid abundance was linked to location in the cave and duration the carrion remained in the cave. The colonization patterns on carrion by troglomorphic differed between permanent and transient cave-dwelling species. Variation could be due to the different reproductive strategies of each species.

Key Words Cave, Phoridae, Leiodidae, carrion, karst, population ecology

Caves have a number of terrestrial microhabitats with patchy food resources including carrion and guano. Carrion in a cave environment is an ephemeral resource generally resulting from the death of accidental cave intruders or bats and crickets (Mohr and Poulson 1966). Faunal surveys in Georgia have noted troglomorphic on carrion but did not discuss the abundance or distribution of these necrophagous species (Holsinger and Peck 1971, Reeves et al. 2000).

Both Poulson and Kane (1981) and Poulson and Culver (1968) conducted preliminary ecological work on carrion communities in caves. Their studies showed that substrate and zone in the cave are important in faunal diversity, but no successional studies were undertaken. Sullivan's (1962) earlier results agreed with their findings. Peck (1975, 1976) used carrion baits to study the abundance of leiodid beetles and the influence of cave entrances on invertebrate populations, but his pitfall traps did not allow a carrion community to develop.

Outside the cave environment, carrion colonization has been studied for forensic and ecological purposes. Several studies show carrion degrades in stages from fresh to dry remains (Payne 1965, Catts and Goff 1992) with different insects characterizing each stage of decomposition. The first objective of our study was to determine if invertebrates attracted to carrion are the same throughout the cave environment and if succession occurs. The second objective was to compare resource use by troglomorphic, troglomorphic, and troglomorphic species. We followed the ecological classification

¹Received 18 September 2000; accepted for publication 15 January 2001.

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criteria of Schiner (1854) as modified by Racovitza (1907) and Barr (1963). Troglotic organisms were considered to be obligate cave dwellers. Troglaphiles, considered to breed and live in cave environments, did not represent obligate cave dwellers. Transient cave dwellers were considered troglonexes.

Materials and Methods

We worked in Sitton's Cave, Dade Co. (N 34°51', W 85°28') and Horseshoe Cave, Walker Co. (N 34°49', W 85°19'), GA, USA. Sitton's Cave is a large cave with more than 4000 m of surveyed passage and an intermittent subterranean stream. Horseshoe Cave is a smaller cave with approximately 250 m of surveyed passage and a permanent subterranean stream.

Chicken liver served as carrion for purposes of our study because cave organisms are seldom specialists and tend to use similar resources as they become available (Mohr and Poulson 1966). Because the carrion associated arthropod fauna is correlated with resource size (Sowig 1997, Catts and Goff 1992), all liver samples were equal in size. To prevent rats from disrupting the experiment, cages (12 × 12 × 1 cm) constructed of flat 1-cm mesh diam galvanized steel-wire were placed over each piece of liver. Forensic entomologists have used cages to exclude large animals from carrion in both terrestrial and aquatic studies (Keiper et al. 1995, Vance et al. 1995).

Each cave was divided into three zones, designated as near an entrance, medium depth, and deep cave. Within each zone, eight pieces of carrion were randomly placed, exclusive of fully aquatic sites. All three study zones were in total darkness. Zone were of approximately equal size within each cave. Caves often have more than one entrance, which are often undiscovered or too small for human access. As a result the distance from an entrance to each zone was not measured. Prior to diving each cave into zones temperature and water levels were measured in each cave bimonthly for a year. Zones were delineated to include regions with no standing or flowing water and similar temperature fluctuations.

Three pieces of carrion were randomly retrieved from each of the three cave zones every week for 2 wks. This sampling pattern was repeated four times from 1997 to 1998. The extra carrion was placed at each zone in case some samples were lost due to unforeseen factors. Identifiable invertebrates were enumerated and removed from the carrion in the field. Unidentified larvae were returned to the laboratory and reared to adults in the dark at 19 to 21°C and 100% relative humidity. Rearing techniques for cavernicolous necrophages were the same as those described by Reeves and Disney (1999).

For each taxon, abundance was analyzed using a three-way ANOVA (unbalanced) with date (week 1, 2), site (Sitton's, Horseshoe), and zone (near entrance, medium, deep) as main effects. A high variance-to-mean ratio indicated a log transformation of the raw data was required (Zar 1996). Data were unbalanced because of stolen equipment, rats, and floods. All statistical tests were considered significant at $P < 0.05$. The abundance of four species were analyzed (Table 2). These were the most numerous species in our study. Other species collected were not numerically significant or represented singletons, and their abundance were not statistically analyzed.

Results

The invertebrate carrion community consisted of 24 species in 19 families of annelids, arachnids, millipedes, insects, and isopods (Table 1). Species were divided

into three functional feeding groups using their known life histories or our laboratory observations: detritivore, opportunistic predator/detritivore, and obligate predator. Eleven species were detritivores, nine species were both detritivores and predators, and four species were predators (including parasitoids) (Table 1).

The abundance of troglophilic phorids (*Megaselia* spp.) (Diptera: Phoridae) did not differ among any of the treatments, whereas cave, zone, date, and the two-way interactions (cave and date, zone and cave, date and zone) were all significantly different for the troglaxene *Calliphora vicina* Robineau-Desvoidy (Diptera: Calliphoridae) (Table 2). This species was present only near the entrance. The troglobitic species, *Ptomaphagus whiteselli* Barr (Coleoptera: Leiodidae), was significantly different in abundance between caves because it did not occur in Horseshoe Cave (Table 2).

Remaining taxa were not collected in sufficient numbers for analysis but appeared to show some segregation in the cave. For example, *Muscina prolapsa* (Harris) (Diptera: Muscidae) was found only in the deep and middle cave zones of Horseshoe Cave and beyond the observed penetration range of *C. vicina* in Sitton's Cave. The major components of the carrion community in Horseshoe Cave were *Megaselia cavernicola* (Brues) and *Me. spelunciphila* Disney, with *C. vicina* existing only as a sporadic component. *Cambala orcha* Chamberlin (Spirasterptida: Cambalidae) was always present in Horseshoe Cave, but populations were not large enough for statistical analyses. The most abundant components of the carrion community in Sitton's Cave were *Me. cavernicola* and *Pt. whiteselli*. Nine other species, including the troglobitic millipedes *Pseudotremia eburnea* Loomis (Chordeumida: Cleidogonidae) and *Scoterpes austrinus* Loomis (Chordeumida: Trichopetalidae), were also common but not numerically large enough for statistical analysis.

Discussion

If the entrance zone is ignored, species diversity in caves is less than that of the surface (Brandon 1962, Poulson and Culver 1968). Culver (1982) believed this "simple," less diverse environment, to be optimal for population-biology studies. The community structure on individual pieces of carrion in Sitton's Cave and Horseshoe Cave was most often characterized by a low species richness. Hundred or thousands of phorids and leiodid beetles were present on the carrion, with 0 to 12 other associated species. For comparison, fetal pigs exposed to insects in South Carolina had 17 to 50 carrion-associated species (Payne 1965). Resource size certainly accounts for some of this difference.

Among aquatic cave fauna, some troglobitic species competing for food resources exclude other troglobites (Culver 1982). Peck (1976) indicated that *Tetracion jonesi* Hoffman (Callipodida: Abacionidae), a troglobitic millipede, might be able to exclude or eat troglophilic and troglobitic competitors. In our study the most abundant troglobitic species, *Pt. whiteselli*, did not appear to exclude troglophiles such as *Me. cavernicola*. The two common troglobitic millipedes in Sitton's Cave, *Ps. eburnea* and *S. austrinus*, were not major components of the community either in number or biomass. Other troglobitic millipedes, like *Te. jonesi*, can be the dominant component of the cave-carrion community in both mass and number (Peck 1976). Likewise, in Horseshoe Cave, the millipedes *Cm. orcha* and *S. austrinus* were not numerically dominant. *Cambala orcha* was an opportunistic predator in the laboratory and thus might feed on

Table 1. Species collected from chicken liver in Horseshoe and Sitton's Caves, Georgia, 1998

Species	April*	August*	September*	October*	Functional group
Oligochaeta					
<i>Aporrectodea</i> sp.	0	H	0	0	Detritivore
Arachnida					
<i>Bishopella laciniosa</i>	S	H/S	S	S	Detritivore/Predator
<i>Liocranoies gertschi</i>	0	H	H	H	Predator
<i>Nesticus georgia</i>	S	S	0	0	Predator
Chordeumida					
<i>Pseudotremia eburnea</i>	0	S	0	S	Detritivore
<i>Scoterpes austrinus</i>	S	H/S	H	H	Detritivore/Predator
Spirostreptida					
<i>Cambala ochra</i>	H	H	H	H	Detritivore/Predator
Isopoda					
<i>Cylisticus convexus</i>	H	H	0	0	Detritivore/Predator
Insecta					
<i>Aspilota</i> sp.	H/S	H/S	S	S	Parasitoid
<i>Calliphora vicina</i>	H	0	0	S	Detritivore/Predator
<i>Cantharis</i> spp.	H	H	H	H	Predator
<i>Corynoptera</i> sp.	0	0	H	0	Detritivore
<i>Leptocera caenosa</i>	0	0	0	H/S	Detritivore
<i>Megaselia cavernicola</i>	H/S	H/S	H/S	H/S	Detritivore
<i>Megaselia spelunciphila</i>	0	H	0	0	Detritivore
<i>Muscina prolapsa</i>	0	H	H	H/S	Detritivore/Predator
<i>Pseudosinella hirsuta</i>	H/S	S	S	S	Detritivore
<i>Psychoda pusilla</i>	0	H	0	0	Detritivore/Predator
<i>Ptomaphagus whiteselli</i>	S	S	S	S	Detritivore
<i>Puliciphora virginiansis</i>	0	0	0	H	Detritivore
<i>Spededophilus littoreus</i>	0	0	0	H	Detritivore/Predator
<i>Tomocerus flavescens</i>	H	H	H	H	Detritivore
<i>Trichocera</i> sp.	H	0	0	0	Detritivore
<i>Xenota</i> spp.	H	H	H	H	Detritivore/Predator

* 0 = no occurrence, H = present at Horseshoe Cave, S = present at Sitton's Cave.

Table 2. Analysis of variance for Phoridae (*Megaselia cavernicola* plus *Megaselia spelunciphila*), *Ptomaphagus whiteselli*, and *Calliphora vicina*. Factors analyzed were cave, date, zone, and two-way interactions. Both Sitton's and Horseshoe Caves, all collection dates, and all zones were analyzed

Source	df	Phoridae		<i>Ptomaphagus whiteselli</i>		<i>Calliphora vicina</i>	
		F	P	F	P	F	P
Cave	1	0.02	0.890	14.93	0.000	20.25	0.000
Date	2	0.44	0.644	1.08	0.343	9.44	0.000
Zone	2	0.04	0.965	0.31	0.732	20.81	0.000
Cave*Date	2	1.55	0.214	2.48	0.870	5.01	0.008
Cave*Zone	2	2.22	0.111	0.62	0.539	9.06	0.000
Date*Zone	4	1.13	0.344	0.20	0.940	6.30	0.000
Error	192						
Total	205						
Mean of							
Abundance	170			17		20	

df = degrees of freedom; F = F value; P = P value.

other carrion species. Hoffman and Payne (1969) indicated that *Cambala* spp. were opportunistic predators.

The most abundant species in both caves were troglomorphic phorids. These flies were found in all zones, but their numbers varied from one adult to 1200 larvae per liver in each zone. Phorid abundance could change rapidly, as shown in the laboratory, phorid eggs can be laid less than 24 h after fly emergence, and larvae pupate in approximately 2 wks (Reeves and Disney 1999). From our results, it is apparent that the phorid population size was independent of date and zone. A similar statement can be made about *Pt. whiteselli* in Sitton's Cave. *Ptomaphagus whiteselli* was present in all the sample zones in Sitton's Cave. These beetles reproduce at a slower rate than the phorids and are recruited to the food resources. Unlike the phorids, *Pt. whiteselli* did not increase its total population in response to the patchy carrion resources. The beetle population on carrion was probably the result of how many beetles could be recruited to a liver before it decomposed. Other invertebrates were potentially important components of the carrion community and contributed between 0 to 5 species to any piece of carrion.

The influence of cave, date, and zone on *C. vicina* populations might be related to oviposition behavior. In both caves, *C. vicina* colonized carrion only near the entrance, did not form permanent cave-dwelling populations, and was affected by seasonal temperature and local weather events. Local surface conditions thus influenced the oviposition behavior, which was indicated by the effects of zone, date, and cave. Similar oviposition behaviors were probably important for other troglomorphic species, such as *M. prolapsa*.

Predatory and parasitic arthropods were collected on the carrion baits. The effects that these species had on popular structure of other cave arthropods are unknown, but Culver (1982) suggested that parasites might be very important in the cave ecosystem. The most common and abundant parasitoid was *Aspilota* sp. (Hymenoptera: Braconidae), a phorid parasitoid. Although not numerous, *Aspilota* sp. might have a significant effect on the behavior and survivorship of its hosts. *Nesticus georgia* Gertsch (Araneae: Nesticidae), a spider with webs near carrion in Sitton's Cave, killed Collembola and *Pt. whiteselli* as they fed on the carrion and wandered into its web. *Bishopella laciniosa* (Crosby and Bishop) (Opiliones: Phalangodidae) was almost always collected on carrion in Sitton's Cave. Like most Opiliones, it is an opportunistic predator and fed on fly and beetle larvae in the laboratory. *Cambala orcha* also fed on phorid maggots in the laboratory and could have influenced carrion-community structure in Horseshoe Cave. Other species were potentially important components of the carrion community.

Few speleologists divide cavernicolous organisms into functional feeding groups. Welbourn (1999) divided the invertebrate cavernicole community into predators, fungivores, scavengers, parasites, and unknown. In the present study, grouping cave-dwelling organisms by feeding behavior was particularly difficult because their life histories are not fully known. For example, although some millipedes are opportunistic predators, those in the genus *Scoterpes* might feed exclusively on fungi and bacteria. Gut contents of *S. austrinus* consisted of sand and bacterially enriched fluids, indicating they fed on liquefied chicken liver. We assumed *S. austrinus* might also feed on other invertebrates. Most cave ecosystems rely on energy from epigeal sources, which consist primarily of woody debris and animal carcasses. In these ecosystems, the detritivores are the most numerous organisms (Conn 1981). Our results support this statement. The detritivores in our study were generalists capable of feeding of a variety of food sources. With the exception of *Aspilota* sp., the predators associated with the carrion community were also generalists. Our data imply that cave communities relying on unpredictable and intermittent food resources are primarily composed of generalists.

Acknowledgments

We thank the Georgia Department of Natural Resources and private land owners for allowing us to collect specimens in their caves. Fieldwork associated with this project was assisted by Clemson University graduate students and faculty and other speleologists including P. H. Adler, C. E. Beard, J. Kintz, E. S. Paysen, B. C. Postlewaite, B. A. Reeves, M. A. Reeves, M. H. Reeves, W. C. Reeves, A. D. Smith, and M. J. Schwallier. Identification of many specimens could not have been made without the assistance of numerous taxonomists. We are grateful for the determinations and helpful comments of the following taxonomists: J. S. Ashe, Staphylinidae; B. V. Brown, Phoridae; J. Cokendolpher, Opiliones; F. Coyle, spiders; R. H. L. Disney, Phoridae; R. Hoffman, millipedes; J. Klimaszewski, Staphylinidae; P. M. Marsh, Braconidae; S. Marshall, Sphaeroceridae; F. Menzel, Sciaridae; S. B. Peck, Leioididae; N. Platnick, spiders; A. Pont, Muscidae; L. Quate, Psychodidae; J. W. Reynolds, earthworms; M. J. Sharkey, Braconidae; W. Shear, isopods; R. Wagner, Psychodidae; and C. Young, Trichoceridae. Fieldwork was partially supported by P. H. Adler and an E. W. King Memorial Grant from the Department of Entomology, Clemson University. This is technical contribution number 4578 of the South Carolina Agriculture and Forestry System.

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