

Community structure of carrion arthropods in the Chihuahuan Desert

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Species numbers, guild, and trophic structure of carrion arthropod communities were examined for 18 mammalian carcasses of varying mass in the northern Chihuahuan desert from May to September 1980. Community structure was described for five carcass weight classes using seven guilds and three trophic levels. Twenty-three carrion-associated species were collected from the carcasses. Large carcasses attracted more species and guilds than small ones. Biomass of necrophagous taxa was higher than predator biomass in all carcass sizes. Linear regression analyses revealed a significant positive relationship between arthropod species richness and carcass mass.

Introduction

It is axiomatic that deserts support fewer consumers than more productive environments (Pianka, 1979). A few studies suggest this may also be true for desert carrion arthropod faunas (Burger, 1965; McKinnerney, 1978). McKinnerney (1978) found only 80 species of arthropods on rabbit carcasses in three different habitats within the northern Chihuahuan desert, whereas Reed (1958) reported 240 species on dog carcasses in a Tennessee lowland forest and Payne (1965) reported 522 species on baby pig carcasses in North Carolina. Therefore, the number of species in carrion arthropod assemblages is dependent on the type of ecosystem in which the test is conducted, and more mesic environments appear to be richer.

Even in the same general area, there can be considerable variability in species composition of carrion communities (Fuller, 1934; Cornaby, 1974). Aside from climatic and seasonal influences, carrion assemblages may exhibit differences in community structure that are dependent on carcass size. In this regard we would expect that smaller, more temporary carcasses should attract and support fewer species of arthropods than larger, more longer lasting ones. In at least a few studies of necrophagous Diptera and Coleoptera there have been attempts to demonstrate the influence of carcass mass on species composition (Kamal, 1958; Denno & Cothan, 1975; Young, 1978). However, unequivocal evidence for this relationship for the total arthropod community awaits further inquiry.

This study is a quantitative analysis of a carrion arthropod community in the summer in the northern Chihuahuan desert. A biomass series of mammalian carcasses was used to determine if communities were similarly structured.

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Study area

The study site was located in El Paso County, Texas (31°56'N, 106°25'W) in the northern Chihuahuan desert (Schmidt, 1979). The site is at 1230 m average elevation. The soil is fine sandy loam underlain by caliche. Arroyos traverse the area. Vegetation is dominated by creosotebush (*Larrea tridentata* [D.C. Cov.]) and honey mesquite (*Prosopis juliflora* [Swartz D.C.]). Precipitation averages 211 mm annually with 60 per cent occurring between July and October. Based on records for a 40-year-period (1940–1980), temperatures have a mean maximum of 34.7°C in June and a mean minimum of 0.1°C in January (N.O.A.A., 1980).

Field methods and materials

Collections and observations of the carrion arthropod community were studied from 18 mammalian baits from May to September 1980. Rodent and rabbit carcasses were sorted into five non-overlapping weight classes and ranged in size from house mice to black-tailed jackrabbits (Table 1).

Table 1. Weight classes, biomass ranges and number of mammalian carcasses used in the study

Weight class	Range (g)	N	Taxon
1	14–18	4	<i>Mus musculus</i> (house mouse)
2	40–55	4	<i>Dipodomys ordii</i> (kangaroo rat)
3	85–290	4	<i>Neotoma albigula</i> , <i>N. micropus</i> (woodrats)
4	630–790	3	<i>Sylvilagus auduboni</i> (desert cottontail)
5	2000–2500	3	<i>Lepus californicus</i> (black-tailed jackrabbit)

Demographic bait traps were used to collect arthropods. Design and fabrication of the trap has been described elsewhere (Schoenly, 1981) only a short summary is provided here. Each trap had eight ingress and four egress funnel assemblies attached around a carrion-enclosing wooden box with 12 sides (Fig. 1). Immigrating and emigrating individuals were collected omnidirectionally from a system of eight killing jars. An anti-freeze solution added to each of the jars was used as a killing and preserving agent (Morrill, 1975). These trap features were intended to minimize disturbance of the community while providing an accurate census of carrion arthropod populations. Five traps were placed on the desert floor and spaced 300 m apart in similar terrain and microhabitat. Carcasses were placed individually in traps and studied until carcass mass reached approximately 80 per cent weight loss. Carcass weight was measured by attaching a Pescola spring scale to a drawstring tied to the carcass and lifting the carcass off the trap floor. Observations of arthropod feeding behaviour were through a central fine net canopy fastened on the trap roof (Fig. 1). Trap jars were emptied between 0900 and 1100 h every other day for up to 14 days. Specimens were deposited in the Resource Collections, Laboratory for Environmental Biology (UTEP).

Analyses

In searching for patterns in community structure we analyzed the carrion community guild composition and trophic structure. In addition to the trap collections, many hours of



Figure 1. Demographic bait trap used to sample carrion arthropod populations. Trap is shown lifted from ground after sampling. The four ingress collection jars are attached to the trap floor; the four egress jars are on the ground. Reprinted with permission from *Environmental Entomology* (copyright 1981) by the Entomological Society of America.

field observation were used to assess feeding behavior and prey selection among the community members. In so observing, we first determined feeding roles to describe guilds (Root, 1967). We then reduced the guilds to two trophic groups, **necrovores and predators**. The carcass formed the third trophic level. Estimates of guild diversity were calculated for carrion arthropods utilizing all carcass size classes by using Simpson's index;

$$D = 1 / \sum_{i=1}^n p_i^2$$

(Simpson, 1949). Small samples from each taxon and life stage (four to seven individuals) were set aside for dryweight biomass estimation. Specimens were oven-dried at 70°C for 48 h and then weighed on a Mettler analytical balance. Individual weights for each species were pooled and averaged. Values of arthropod biomass for each taxon were obtained by calculating the product of mean-weight and the average number of individuals for each weight class. Regression and correlation analyses were used to find relationships between carcass mass, arthropod species richness, and arthropod guild proportions.

Results and discussion

In general, all carcasses showed periods of active and advanced decomposition with a strong odor of decay. For jackrabbit carcasses, our results as to arthropod succession, stages of decomposition, and arthropod families represented generally concur with those reported by McKinnerney (1978).

Species and guilds

A total of 28 arthropod species was collected from the traps during the 5-month-period. Of these, 23 species were identified as carrion community participants, **utilizing information from field observations and published accounts** (Howden, 1950; Reed, 1958; Payne, 1965; Johnson, 1975; McKinnerney, 1978). Based on this information each of the 23 species was assigned to one of seven guilds (Table 2). Only the solpugid *Eremobates marathoni*, and the tenebrionids, *Eleodes carbonarius*, *E. longicollis*, and *Embaphion* sp., were unique to the desert carrion fauna when compared with species inventories from other, non-arid environments (for example: Reed, 1958; Payne, 1965; Johnson, 1975). This is not surprising,

Table 2. *Guilds of the carrion arthropod community*

Abbreviation	Description of carrion arthropod
(CF)	Carcass fluid feeders Sarcophagidae: <i>Blaesoxipha plinthopyga</i> (Wiedemann) Calliphoridae: <i>Cochyliomyia macellaria</i> (Fabricius) Muscidae: <i>Musca domestica</i> L.
(IC)	Intestinal contents feeders Scarabaeidae: <i>Boreocanthion puncticollis</i> (LeConte)
(MI)	Muscle and internal organ feeders Dermestidae: <i>Dermestes marmoratus</i> Say Diptera larvae Tenebrionidae: <i>Eleodes carbonarius</i> (Say), <i>E. longicollis</i> LeConte, <i>Embaphion</i> sp.
(NP)	Necrophagous-predaceous forms Silphidae: <i>Silpha truncata</i> (Say), <i>Necrophorus marginatus</i> Fabricius Formicidae: <i>Conomyrma bicolor</i> (Wheeler), <i>Pheidole</i> sp., <i>Novomessor cockerelli</i> (André), <i>Crematogaster clara</i> Mayr, <i>Iridomyrmex pruinosum</i> (André)
(SL)	Skin, ligament, and sinew feeders Trogidae: <i>Trox suberosus</i> Fabricius
(SP)	Specific predators and parasitoids Histeridae: <i>Saprinus discoidalis</i> LeConte Pompilidae: <i>Aporinellus</i> sp., <i>Cryptocheilus terminatum</i> (Say)
(GP)	General predators Solpugida: <i>Eremobates marathoni</i> Muma Araneida: <i>Syspira longipes</i> (Simon), <i>Psilochorus utahensis</i> Ch. Staphylinidae: <i>Creophilis maxillosus</i> (Linné)

however, since both solpugids and darkling beetles are conspicuous elements of arid and semi-arid environments (Crawford, 1981).

Muscoid flies are direct fluid feeders on the carcass and are represented by sarcophagids (flesh flies), muscids (house flies), and calliphorids (blow flies). The blow fly, *Cochliomyia macellaria*, was the most abundant species represented (1381), followed by the flesh fly, *Blaesoxipha plinthopyga* (218), and the house fly, *Musca domestica* (51). Adult dipterans were collected in high numbers shortly after carcass deposition (days 2–4) when tissues were fresh and at a time when the carcass presumably reached peak levels of attractiveness for feeding, oviposition, and larviposition (Table 3). It was only after advanced carcass decay (days 6–8) had begun that a rapid decline in numbers of adult flies was observable. This pattern was especially noteworthy in rabbit carrion.

The feeders on intestinal contents included only the dung rolling beetle, *Boreocanthion puncticollis*. Dung beetles were collected in small numbers (14) only from the heavier rabbit carcasses, and their time of activity ranged from 2–10 days (Table 3). Similarly,

Table 3. Number of carrion associated arthropods collected from mammal carcasses in the northern Chihuahuan desert from May to September 1980

		Weight class 1 (14–18 g) House mice (<i>n</i> = 4)					Weight class 2 (40–55 g) Kangaroo rats (<i>n</i> = 4)					Weight class 3 (85–290 g) Woodrats (<i>n</i> = 4)				
Taxa and guilds	Days	2	4	6	8	Total	2	4	6	8	Total	2	4	6	8	Total
Hymenoptera																
Formicidae (NP)		221	111	187	38	557	18	19	27	30	94	228	75	23	—	326
Pompilidae (SP)		—	3	—	—	3	—	1	1	—	2	—	—	—	—	0
Diptera																
Muscoid flies (CF)		—	—	6	—	6	—	2	1	—	3	—	8	4	4	16
dipteran larvae (MI)		—	—	—	—	0	—	—	—	—	0	—	147	—	—	147
Coleoptera																
Tenebrionidae (MI)		—	1	—	—	1	—	—	3	2	5	—	—	—	—	0
Histeridae (SP)		—	—	—	—	0	—	4	1	—	5	26	10	—	—	36
Araneida (GP)		4	1	1	—	6	4	5	3	2	14	1	2	2	—	5
Solpugida (GP)		1	1	—	—	2	—	—	—	1	1	1	2	—	—	3

		Weight class 4 (630–790 g) Desert cottontails (<i>n</i> = 3)						Weight class 5 (2000–2500 g) Blacktailed jackrabbits (<i>n</i> = 3)								
Taxa and guilds	Days	2	4	6	8	10	12	Total	2	4	6	8	10	12	14	Total
Hymenoptera																
Formicidae (NP)		39	107	406	83	250	4	889	149	31	60	127	350	139	44	900
Diptera																
Muscoid flies (CF)		—	46	82	37	—	1	166	579	57	520	8	37	4	189	1394
dipteran larvae (MI)		—	49	17	221	49	2	338	—	24	249	856	229	68	7	1433
Coleoptera																
Tenebrionidae (MI)		—	1	—	—	—	—	1	—	1	—	—	—	—	—	1
Histeridae (SP)		26	93	65	35	15	5	239	41	213	119	59	24	23	4	483
Trogidae (SL)		—	6	3	1	—	1	11	—	28	22	13	2	2	—	67
Dermestidae (MI)		2	26	10	17	2	4	61	—	28	74	22	20	6	5	155
Staphylinidae (GP)		—	1	—	—	—	—	1	—	1	4	2	—	—	—	7
Silphidae (NP)		—	1	1	—	—	—	2	—	5	3	—	—	—	—	8
Scarabaeidae (IC)		—	—	1	—	2	—	3	1	9	1	—	—	—	—	11
Araneida (GP)		3	—	—	2	7	2	14	—	5	1	5	4	1	—	16
Solpugida (GP)		3	3	3	—	2	1	12	3	1	1	3	—	1	—	9

McKinnerney (1977), using hunted rabbits, reported *Boreocanthion lecontei* exploiting intestinal contents from day 1 to 11.

Dermestid and tenebrionid beetles and dipteran larvae are indiscriminate feeders in the carcass interior. We observed dermestids entering rabbit carcasses as early as day 2 when viscera and muscle tissues were still intact. Shortly afterward, initiation of dipteran larval emigration from the carcasses was recorded (Table 3). Dipteran larvae reached their highest levels of emergence from jackrabbit carcasses (total 1433) during periods of active and advanced decomposition (>4 days). Emigrating larvae from cottontail and woodrat carcasses were recovered in relatively smaller numbers (338 and 147, respectively). Despite their conspicuous presence in the habitat, darkling beetles were recovered in very small numbers but from all carcass sizes (8). In addition to carcass utilization, tenebrionids feed on a variety of other materials (Crawford, 1979).

Ants and adult silphid beetles are omnivorous, feeding both as necrovores and predators. At the onset of carcass availability ants are necrophilous and exhibit some fly egg predation. Ants preyed on fly larvae as soon as the latter were present. Silphids arrived at rabbit carrion on the fourth day and began feeding on tissues and maggots.

Trogid beetles are reported as feeders on dried skin, ligaments, and sinews (Vaurie, 1955). Trogids were collected from rabbit carcasses as early as day 4 and continued to appear until the termination of each trial (Table 3). Like dermestids, silphids, and scarabs, trogid beetles were found only on rabbit carrion (total 78).

Histerid beetles and parasitic hymenopterans are specific predators in the carrion community. Histerids were observed feeding on dipteran larvae as early as day 4. The pompilid wasp species, *Cryptocheilus terminatum*, and *Aporinellus* sp., are considered host specific spider parasitoids (Krombein, Hurd *et al.*, 1979).

General predators included spiders, staphylinids, and solpugids. Staphylinid beetles were observed preying on dipteran larvae and other insects (flies and smaller beetles); spiders were general dipteran predators. Muma (1966) reports solpugids as general insect predators with some restrictions on size and thickness of prey cuticle. During the collection period 13 solpugids were recovered from the traps. However, because of their nocturnal habits no definite observations on feeding behavior in the carrion community were assessed.

Guild structure

As indicated by the increasing values of guild diversity, the heavier carcasses (e.g. rabbits) attracted and supported more guilds (Table 4) and greater numbers of carrion arthropod species and individuals than smaller carcasses (Table 3). Guild diversity also increased in larger carcasses in response to a more even distribution of arthropod numbers in all the guilds. The relationship between guild diversity and carcass size classes was significant ($r = 0.888$, $P < 0.05$).

Ants and muscoid flies were numerically the most dominant and most generalized carrion utilizers of all the groups considered (grand totals for all carcasses were 2776 and 1585, respectively). Their dominance in the community stemmed largely from their high density in the habitat and early arrival time at the carcasses. Proportions of muscoid flies were positively correlated with increasing carcass size ($r = 0.999$, $P < 0.001$), whereas ants were proportionately more abundant on smaller carcasses than on larger ones ($r = -0.900$, $P < 0.02$). The latter relation supports observations made by Matthews (1976) in his study of arthropods on small vertebrate carrion in Australia. Among the Coleoptera assemblage, hister beetles were found in all but the smallest size class, while dermestids, trogids, staphylinids, scarabs, and silphids were recovered only on rabbit carrion (Table 3).

Dipteran larvae were collected from woodrat and rabbit carrion but were absent from the smaller carcasses. The absence of maggots from mouse and kangaroo rat carcasses, despite the presence of adult dipterans, may be attributed to several factors: (1) carcass desic-

Table 4. Percentages of arthropods within each guild and guild diversity estimates for five carcass weight classes

Guild	House mice (WC1)	Kangaroo rats (WC2)	Woodrats (WC3)	Cottontails (WC4)	Jackrabbits (WC5)
Carcass fluid feeders (CF)	1.04	2.41	3.00	9.55	31.08
Intestinal contents feeders (IC)	0	0	0	0.17	0.24
Muscle & internal organ feeders (MI)	0.17	4.03	27.57	23.02	35.43
Necrophagous-predaceous forms (NP)	96.86	75.80	61.16	51.29	20.25
Skin, ligament & sinew feeders (SL)	0	0	0	0.63	1.50
Specific predators & parasitoids (SP)	0.52	5.64	6.75	13.75	10.77
General predators (GP)	1.39	12.09	1.50	1.55	0.71
Guild diversity ($D_{\max} = 7$)	1.06	1.68	2.19	2.91	3.63

Table 5. Average standing crops of arthropod biomass (g) within each trophic category and ratios of predator/detritivore biomass (%) for five carcass weight classes.
(See text for details)

Trophic level	House mice (WC1)	Kangaroo rats (WC2)	Woodrats (WC3)	Cottontails (WC4)	Jackrabbits (WC5)
Secondary consumers (predators and parasitoids)	0.12	0.04	0.20	1.60	3.30
Primary consumers (necrovores and detritivores)	0.14	0.20	1.10	5.50	29.30
Mean carcass mass	16	48	185	710	2250
Predator/detritivore ratio (%)	86	20	18	29	11

cation; (2) an inadequate food base; or (3) predation by ants. Since no ant-maggot encounters were witnessed in small carcasses, we reject the third possibility. We suggest, therefore, that the existing high temperatures and low humidities accelerated fluid loss from carcasses, thereby reducing the food base and the time available for larval and pupal maturation. This was supported by the fact that mouse carrion lost weight at a faster rate than rabbit carrion (70 per cent versus 45 per cent in 4 days, respectively).

Trophic structure

Table 5 shows the three trophic levels: carcass, primary consumers (detritivores and necrovores), and secondary consumers (predators and parasitoids). Since ants and silphid beetles feed at both trophic levels, their numbers were arbitrarily divided equally between both consumer levels. The detritivore component was gathered from five guilds (CF, IC, MI, NP, SL, see Table 2), while three predator guilds were combined to form the third level (NP, GP, SP).

In general, carcasses supported a lower biomass of predators than detritivores. Young (1978) reported a similar relationship in his study of carrion assemblages inhabiting a Costa Rican neotropical forest. Moreover, our data show that the ratio of standing crop of predators to detritivores tends to decrease in larger carcasses. In the mouse carcasses, mean biomass of predators was 0.12 g compared with a mean of 0.14 g for detritivore biomass. This yielded a ratio of predator to detritivore biomass of $\approx 1:1$. By comparison, jackrabbit carrion supported a mean biomass of predators of 3.3 g compared with a mean of 29.3 for detritivores, yielding a ratio of predator to detritivore biomass $\approx 1:10$ (Table 5). The relatively high standing crop percentage in weight class 4 is attributable to a proportionately larger number of predaceous beetles to carrion feeders. With a 140-fold difference in the range of carcass weight (16–2250 g), detritivore biomass displayed a significant 208 fold increase ($r = 0.992$, $P < 0.001$) ranging from 0.14 g to 29.3 g. This dramatic increase in detritivore biomass was principally attributable to maggots. In woodrat, cottontail, and jackrabbit carcasses, dipteran larvae accounted for 81, 53, and 44 per cent of the total detritivore mass. Secondary contributions were made by trogid and dermestid beetles. Alternately, predator biomass significantly increased only 27 times from 0.12 g to 3.3 g ($r = 0.983$, $P < 0.001$). Hister beetles were the major contributors, accounting for 37, 62, 71, and 69 per cent of the total predator biomass in weight classes 2, 3, 4, and 5.

It is appropriate to consider the temporal effect of carcass availability on arthropod standing crops. The duration of carcass availability (based on 80 per cent weight loss) ranged from 8 days for mouse and rat carcasses to 14 days for jackrabbit carrion (Table 3). Therefore, the weight classes of carcasses used in this study exhibited differential rates of decomposition; smaller carrion decomposed and desiccated at a faster rate than larger ones. The availability of rabbit carcasses for 4–6 days longer than others presumably increased both the survival rate and developmental period for emerging larvae and increased the location time for searching arthropods. Analysis of the importance of slower decomposition rates in larger carcasses to arthropod standing crops revealed variable results. If just ants are considered, the extended period accounted for 28 per cent of the total formicid biomass for cottontail carcasses (days 10–12), and 59 per cent for jackrabbit carcasses (days 10–14). Secondary contributions by other taxa like dipteran larvae (15 per cent for weight class 4, 21 per cent for weight class 5), dermestids (10 and 20 per cent), and histerid beetles (8 and 11 per cent) were also noteworthy.

Species-carcass size relations

When the number of carrion arthropod taxa is plotted against the logarithm of the initial mass for each of the 18 carcasses (Fig. 2), a significant increase is observed ($Y = -0.03 +$

$1.69 \ln [X]$, $r = 0.770$, $P < 0.001$). This indicates that at least as far as carrion communities in the summer in the Chihuahuan desert are concerned, there is a strong correlation between carcass mass and arthropod species richness. Whether this relationship stems from an increase in attractive value of large versus small carrion, or from an increase in carcass availability time, as in rabbit carrion, is not clear. However, close re-examination of Table 3 reveals that regardless of carcass size, the complete complement of taxa was collected by the end of the sixth day. Therefore, we posit that the attractive power of carcasses is more influential in affecting species richness of carrion arthropods than the duration of carcass availability.

It is reasonable to assume that as in other communities, there is some maximum number of carrion arthropod species that the surrounding habitat can support, and that the relation

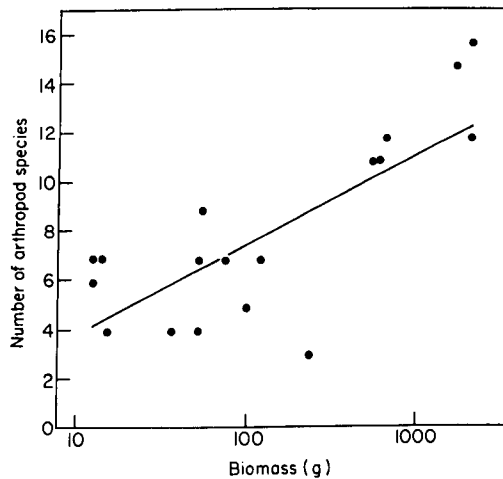


Figure 2. Relationship between number of carrion arthropod species and carcass mass ($N = 18$).

should therefore approach an asymptote (Archibald, 1949; Vestal, 1949). A function of the form:

$$\text{Species in carcass} = \text{max. in general habitat} [1 - a \times \exp(-bm)],$$

where a and b are constants and m is initial biomass might be a more adequate model. This expression implies that some fraction, $1 - a$, of the potential species would be caught in an unbaited trap. The constant b relates species richness to carcass mass. Assuming the 23 species collected on all 18 carcasses represent the maximum number of carrion arthropod taxa for this habitat, season, and carcass biomass range, we obtained:

$$\text{Species} = 23[1 - 0.74 \times \exp(-0.0031m)], r = 0.870, P < 0.0001.$$

Qualitatively, the progression of arthropod taxa followed an orderly sequence in carcasses of increasing mass (Table 3). Besides the ant fauna, which was an important component in all carcass sizes, other arthropods attracted to small carcasses (weight classes 1 and 2) included spiders, solpugids, tenebrionids, sarcophagids, and parasitic hymenoptera (mean number of taxa = 6.0 species). With the exception of tenebrionids and pompilid wasps, all of the above groups plus calliphorid flies, histerid beetles and dipterous larvae were found in woodrat carcasses (mean 5.5 species). Rabbit carcasses (cottontails

and jackrabbits) attracted all the aforementioned taxa plus muscid flies, trogid, staphylinid, silphid, and scarab beetles (mean 11.3 and 14.3 species, respectively).

The apparent preference of silphid, staphylinid, scarab, and trogid beetles for rabbit carcasses may be due to their having less ability to locate smaller carrion and a lower local density of beetles relative to ants and flies.

Studies of carrion beetles in forest habitats (Shubeck, 1968, 1975) have shown that the detection of carrion by silphids from a variety of distances (5–75 m) was due not to odor orientation but rather to random wandering; the limit of odor perception was approximately 1 m from the carrion source. In addition, some silphids and histerids apparently locate carrion without the aid of visual senses, whereas some staphylinids rely on both visual and olfactory organs. Therefore, the restriction of air flow around concealed carcasses enclosed by traps, relative to carcasses in the open, may have lowered the threshold of small carcass detection for carrion beetles. The greater attractiveness of rabbit carrion may have contributed to an increase in numbers and species of beetles.

Conclusions

Several general conclusions can be drawn from this study. Numbers of carrion-feeding species and arthropod feeding guilds increased in a relatively orderly manner with increasing carcass size. The larger carcasses attracted a more diverse consumer community; larger proportions of ants and no larvae were supported in small carcasses. More individuals and species of beetles were found on rabbit carcasses; only histerids and tenebrionids were recovered from small carrion. The increasing response of arthropod taxa to larger carcasses may be due to an increase in carcass attractive value rather than to temporal effects of carcass availability. Hence, desert carrion arthropods form well-structured communities related to resource size.

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