CARRION COMMUNITIES IN THE NORTHERN CHIHUAHUAN DESERT

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ABSTRACT. Carrion community composition was examined in 40 rabbit carcasses at three northern Chihuahuan Desert study areas in Texas and New Mexico from May to August, 1976. Four seral stages of decomposition are described for the carcasses: Fresh, Active, Advanced Decay, and Dried. Of 80 arthropod species collected, 63 are identified as participants in the carrion community. Six vertebrate forms were participants. Probable feeding roles of arthropod and vertebrate taxa are presented. Diversity and concentration of dominance were calculated for seral stages, and relationships to resource diversity and food chain complexity are discussed. Removal efficiency of vertebrates and colonization efficiency of arthropods are correlated to describe a probable abbreviation of arthropod carrion communities in small carcasses; possible implication for arthropod adaptations are presented. No direct correlation appeared between carrion community composition and area meteorological conditions.

Tissues of dead animals provide a food source within ecosystems, supporting a population of consumers that include decomposers and invertebrate and vertebrate animals. This consumer population may in turn support associated populations of predators and parasites, producing a "microcommunity" (Reed 1958).

Previous investigations of carrion communities have focused largely upon carrion insects (Motter 1898; Illingworth 1926; Brannon 1934; Fuller 1934; Kaufmann 1937; Howden 1950). Behavior and food habits of vertebrate scavenger species also are well-known for vultures (Parmalee 1954; Stager 1964) and coyotes (Murie 1951; Rogers 1965). The role of microbes in processing animal tissue has been extensively investigated (Elkan and Moore 1960; Okafor 1966; Wahlquist 1971; Cahenzli 1975). More comprehensive studies of the carrion microcommunity conducted in the eastern United States by Reed (1958), Payne (1965), and Johnson (1975) have ad-

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dressed stages in decomposition, insect community succession, and the influences of meteorological conditions upon carrion insects.

This study presents an analysis of the animal carrion community of the northern Chihuahuan Desert: (1) identity of carrion community species; (2) nature of each species' role in the carrion community patterns; and (3) occurrence and characteristics of carrion community seral stages, including species numbers and diversity, and correlated carcass age and stage of decomposition. This analysis is based upon field observations of carcass baits at three Chihuahuan Desert sites during May-August, 1976.

STUDY AREAS AND METHODS. Observations were conducted at the following study areas: (1) Walters Ranch, White Sands National Monument, Otero County, New Mexico; (2) Aden Crater, Dona Ana County, New Mexico; and (3) a site in the Hueco Mts., approximately 23 miles east of El Paso, El Paso County, Texas. The Walters Ranch area includes marginal gypsum sand dunes and interdunal zones and extensive saltbush flats. Aden Crater is a volcanic cone surrounded by a large area of lava flows and eolian sand deposits. The Hueco Mts. site is an area of arroyos and bajadas at the edge of the Diablo Plateau.

Black-tailed jack rabbits (*Lepus californicus*) and desert cottontail rabbits (*Sylvilagus auduboni*) obtained by hunting were used as carcass baits. Carcasses were placed approximately 350 m apart and secured by a 30 cm tent stake driven through the shoulder region and into the ground. Seventeen carcasses placed at Walters Ranch on 21, 22, and 23 May were observed daily (0700-1000) for 30 days and periodically for an additional seven weeks. Twenty carcasses were placed at Aden Crater on 11 July and observed daily (0700-1000) for five days. Specimens of arthropods occurring at the carcasses were collected using insect net and forceps. Observations were recorded of arthropod numbers and activities, vertebrate tracks occuring at carcasses, disturbance and state of carcass tissue, and sightings of vertebrate scavengers. Three carcasses were placed at the Hueco Mts. site on 27 July inside enclosures measuring approximately 0.6 m in diameter and 40 cm in height and constructed of 2.5 cm mesh net wire. This measure eliminated the effects of vertebrate scavengers. Twice daily observations (at 0700 and 1600) were conducted for 15 days and daily morning observations continued for an additional 11 days. One evening observation (at 2100) was conducted on 9 August. Minimal numbers of arthropods were collected to avoid disturbance of the carcass community.

Diversity for seral stages was calculated by the Shannon-Weaver index of general diversity (H'),

$$H' = - \sum_{i=1}^{s} P_i \ln P_i$$

where s is the number of taxa as listed for the seral stage and P_i is the proportion of the total number of individuals of the ith taxon (Poole 1974). P_i was estimated by assigning the following values to each category of population size: single=1, small=5, and large=30. Each vertebrate species was assigned a value of 1 in

calculating P_i. Similarity between seral stages was calculated by the index of similarity (S),

$$S = \frac{2C}{A+B}$$

where A is the number of taxa in stage A, B is the number of taxa in stage B, and C is the number of taxa common to both stages (Odum 1971). Concentration of dominance was calculated by the index of dominance (c),

$$c = \Sigma (n_i/N)^2$$

where n_i is the importance value for a taxon (number of individuals, as assigned in calculation of diversity) and N is the total of the importance values for the stage (total number of individuals).

RESULTS AND DISCUSSION. The decomposition of carcasses has been divided into various numbers of stages by different workers. Reed (1958) and Johnson (1975) described four stages and Payne (1965) used five stages, while Howden (1950) defined only two stages based upon dipteran life cycles. The penetration of the body cavity by the stake securing my carcasses eliminated the bloating stage noted by other workers. The following is a description of the seral stages recognized for the carcasses in this study, based upon significant features of carcass decomposition. The taxa associated with each stage represent a summarization of the appearance of all taxa at all sites. The days designated for each stage are an average for all carcasses and sites. Taxa preceded by + occurred in moderate to large numbers during the stage.

Fresh Stage (Days 1-2)

During this period the body appeared fresh, with no escape of fluid except the blood released when the stake was driven through the body. No odor of decay was detected. The eyes and associated membranes usually were eaten during this period by ants.

Taxa present included: +Formicidae, +Calliphoridae, +Sarcophagidae, +Trogidae, +Otitidae, +Histeridae, +Scarabaeidae, Tenebrionidae, Muscidae, Tachinidae, *Canis latrans, Urocyon cinereoargenteus, Carthartes aura, Mephitis mephitis/Conepatus mesoleucus.*

Active Stage (Days 3-15)

During this period fluids began to escape from the body at the anal opening, mouth, nose, and eyes and from viscera through holes in the abdominal wall underneath the body. The quantity of insects present caused the carcass to vibrate with the activity and sounds of the inhabitants. The fur began to loosen from the skin in patches.

The odor became progressively stronger, reaching a peak on days 6-7, then decreasing. Near the end of this period, maggots left the carcass in great numbers, often literally covering the ground around the carcass.

Taxa present included: +Formicidae, +Calliphoridae, +Sarcophagidae, +Trogidae, +Otitidae, +Histeridae, +Dermestidae, +Silphidae, +Scarabaeidae, +Muscidae, +Tachinidae, +Piophilidae, +Staphylinidae, Tenebrionidae, Anthomyiidae, Cleridae, Braconidae, Carabidae, Phalangidae, Reduviidae, Asilidae, Araneidae, Apidae, Vespidae, Andrenidae, Nitidulidae, Tephritidae, *Canis latrans*.

Advanced Decay Stage (Days 16-30)

By this time, the carcass odor had almost completely disappeared and fluid had ceased escaping from the body, although some moisture remained in the tissue. Most of the fur dislodged from the skin and lay matted around the edge of the carcass. The only skin areas which sometimes retained fur were feet, legs, and ears. Numerous holes appeared in the outer surface of the exposed abdominal area. When lifted, the opposite abdominal wall was observed to have disappeared, along with most of the viscera.

Taxa present included: +Formicidae, +Trogidae, +Staphylinidae, Calliphoridae, Sarcophagidae, Otitidae, Tenebrionidae, Cleridae, Histeridae, Muscidae, Dermestidae, Piophilidae, Halictidae, Tachinidae, Tephritidae, Acrididae, *Canis latrans*.

Dried Stage (Days 30-)

The division between advanced decay and dried stages is rather indefinite, marked mainly by the appearance of bare bones. This feature may appear much earlier through the action of vultures. This stage was observed only at the White Sands study area (two carcasses) and is best characterized by the disappearance of most of the carrion community. Any skin and tissue remaining was shriveled, dried and blackened, and separated from bones. The bones eventually separated and the incisor teeth fell from the skull.

Taxa present included: Formicidae, Otitidae, Calliphoridae, Sarcophagidae, Trogidae, Histeridae.

General diversity (H') for each seral stage is shown in Table 1. Species diversity has been related to a variety of factors, of which several appear functional in the carrion community. Diversity of the resource influences the number of species able to utilize that resource through various partitioned feeding patterns of the species (MacArthur 1972). Resource partitioning by necrophagous taxa

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TABLE 1

General diversity (H') and concentration of dominance (c) indices for seral stages of carrion communities.

Index	Stage 1	Stage 2	Stage 3	Stage 4
General diversity	2.0599	2.8281	2.2058	1.529
H'	±0.3122	±0.0347	±0.0832	±0.0082
Concentraton of				
Dominance (c)	0.1370	0.0645	0.1421	0.2

does occur in the carrion community. The status of the carcass during stage 2 features a maximum diversity of food material available to arthropods. The fresh carcass during stage 1 offers food mainly to surface-feeders. The action of maggots and bacteria affect accessibility to the internal tissues for many stage 2 species featuring feeding preferences for internal products and/or morphological specializations for use of internal tissues. The diversity of the carcass material decreases following stage 2, as the feeding of the inhabitants rapidly reduces all portions of the resource.

Odum (1971) states that increasing complexity of feeding relationships is positively correlated with species diversity. Stage 2 features the greatest complexity of feeding relationships, produced mainly by the appearance of numerous predatory arthropod taxa and the exercise of alternate prey selection by some generalists, such as the formicids. Thus at stage 2, the carcass offers a maximum of available food and the necrophagous taxa utilizing the resource support a population of predatory and parasitic taxa. Predation and parasitism focus mainly upon maggots which are present almost exclusively during stage 2. Again, the relative simplicity of food chains in other stages is reflected in the diversity indices.

The indices of similarity (S) for the four seral stages show that stages 1, 2, and 3 were most similar, with greatest similarity between stages 2 and 3. This agrees with the diversity indices for the stages, and emphasizes the increase and decline of the resource diversity and food chain complexity.

Indices of concentration of dominance (c) are shown in Table 1. Stage 4, with almost complete evenness between taxa, exhibits the largest (c). Stage 2 includes a few taxa with high importance and thus exhibits the smallest concentration of dominance. This agrees with the expected negative correlation between diversity (H') and concentration of dominance.

A total of 80 species of arthropods was collected, of which 63 species were identified as participants in the carrion community, based upon field observations and information on feeding habits obtained from the literature. Six vertebrate forms also were identified as participants.

Participant arthropod species were grouped in major taxonomic categories and the occurrence of major taxa was summarized for each study area (Figs. 1, 2, and 3). Community composition at each study area was compared to local humidity, temperature, and rainfall records. No significant correlations could be identified between carrion community composition and general meteorological conditions. Previous workers have noted that community composition is most directly influenced by the carcass microclimate, which may vary considerably from weather conditions of the general area.

Shown in Fig. 4 is a food web depicting the probable feeding relationships between taxa of the carrion community. Several of the taxa can be described as sporadic in occurrence at the carcasses, appearing in small numbers or in single individuals in brief visitations to the carcasses. These include braconid and vespid wasps,
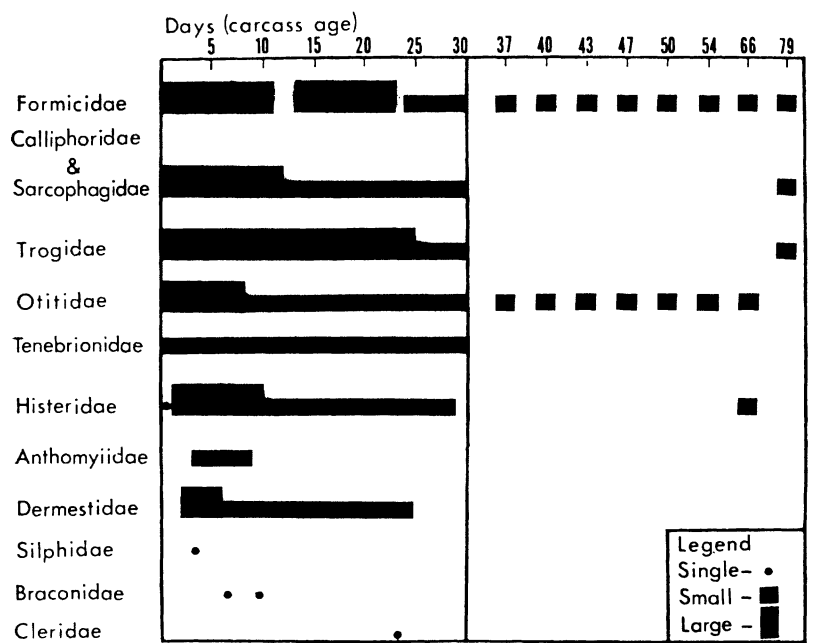

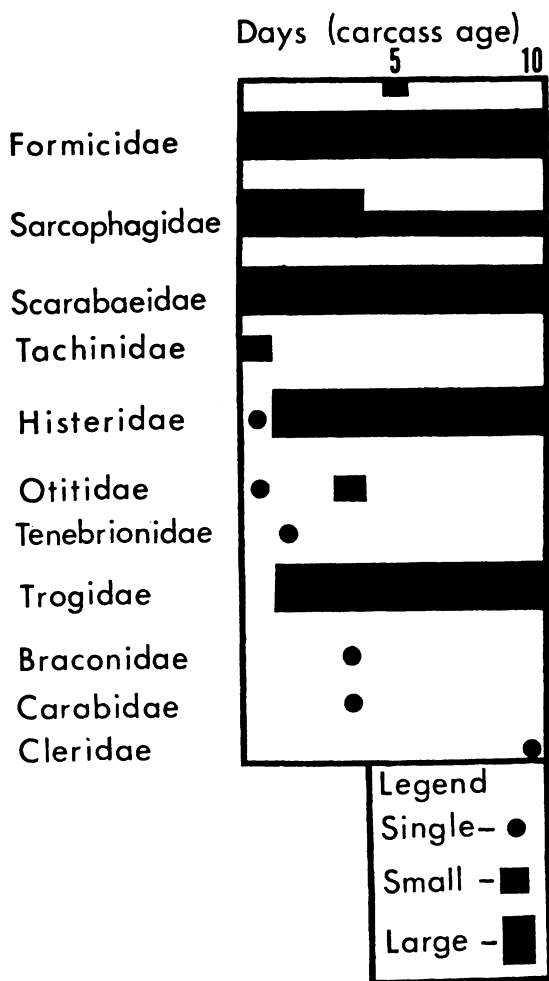Fig. 1. Community composition at White Sands study area.

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Fig. 2. Community composition at Aden Crater study area.

honeybees, panurgid bees, spiders, harvestmen, grasshoppers, carabid and nitidulid beetles, robberflies, reduviid bugs, and tephritid flies. Occurrence of members of this sporadic category is best described as opportunistic in nature, implying ability of these forms to secure their specific food requirements from a variety of sources, including carrion.

Although carrion is portrayed as a single resource in the food web, considerable partitioning of this resource occurred through specific preferences of various taxa. Thus among the necrophagous
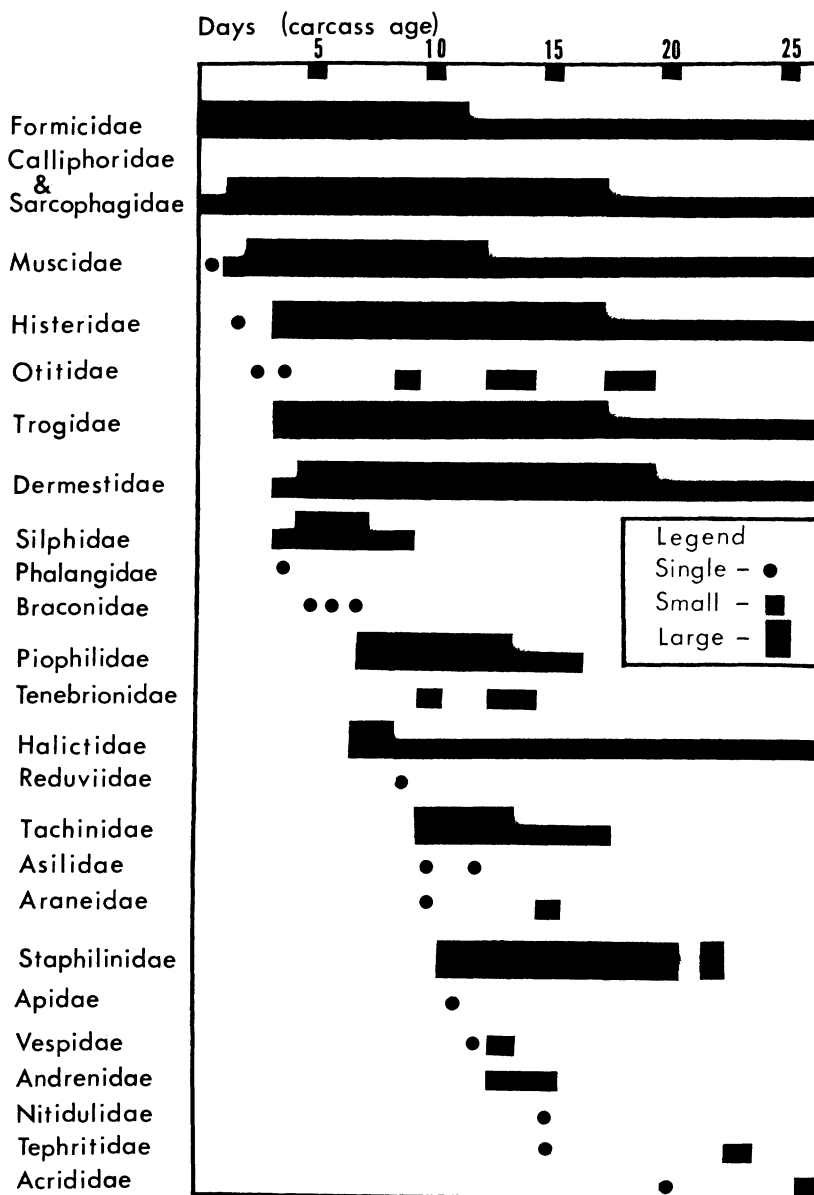
Fig. 3. Community composition at Hueco Mts. study area.

CARRION

Cleridae
Histeridae
Braconidae
Tachinidae
PREDACEOUS
(specific)

Calliphoridae
Sarcophagidae
Dermestid larvae
other Coleopteran larvae
Dipteran larvae
Dermestidae
Acrididae
Apidae
Vespidae
Nitidulidae
Trogidae
Tenebrionidae
Scarabaeidae
Lepidoptera
Otitidae
Tephritidae
Piophilidae
Anthomyiidae
Muscidae
Andrenidae
Halictidae
Canis latrans
Urocyon cinereoargenteus
Cathartes aura
Bubo virginianus

NECROPHAGOUS

Formicidae
Silphidae
Phalangidae
NECROPHAGOUS–
PREDACEOUS

Reduviidae
Carabidae
Asilidae
Araneidae
Staphylinidae
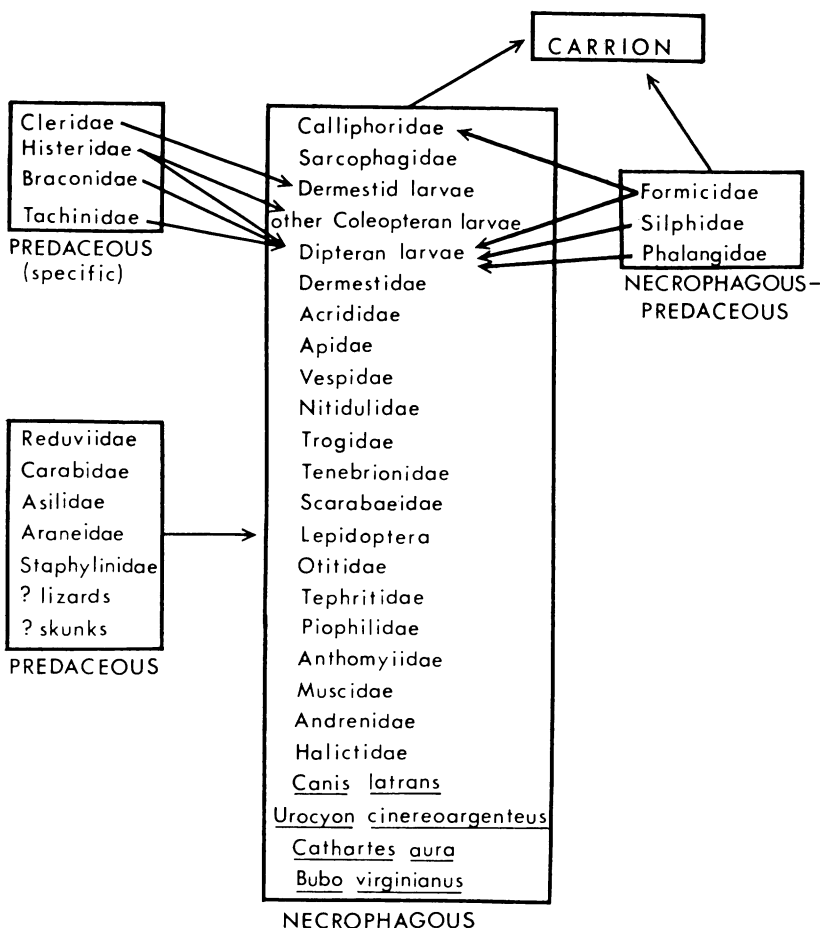? lizards
? skunks
PREDACEOUS

Fig. 4. Probable relationships of feeding roles in the carcass community.

taxa are those which utilized mainly carcass fluids (Vespidae, Lepidoptera), muscle and internal organs (dipteran larvae), skin and ligaments (Trogidae), fur (Acrididae), and intestinal contents (Scarabaeidae). In the necrophagous category, dermestids and trogid beetles are limited mainly to carrion usage; even muscoid flies utilize alternate resources such as dung and decaying vegetable materials.

The formicids are the best represented group among the necrophagous-predaceous population, yet these must also be considered opportunistic. The silphid beetles are largely carrion specialists.

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Most of the predaceous forms also are opportunistic, with the exception of the hister beetles, which are mainly found in association with decomposing tissue or dung.

Population dispersal of the carcass community included immigration (initial colonization), migration (diel periodicity among some forms and sporadic visitation by others), and emmigration (abandonment of carcass in late stages). Rates of dispersal are greatly influenced by the movement capabilities of the species (vagility) and the existence of barriers to dispersal (Odum 1971). In application to the efficiency in immigration for both vertebrate and arthropod species, vagility can be enlarged to include not only motility, but also means of food location and density of the species in the general habitat. Formicids and muscoid flies, forms with extremely different means of movement, exhibited the greatest colonization efficiency, finding the carcass within hours after placement. Both forms are observed to engage in wide dispersal in the habitat in search of food, not depending solely upon long-distance, chemo-sensory attraction to locate suitable food. Both forms also exhibit high density within the habitat. By comparison, hister and silphid beetles have been shown by Shubeck (1971) to locate carrion at least partially by the odor of decay, and their densities in the general habitat are very low. Milne and Milne (1976) noted arrival of burying beetles at a fresh carcass within 35 minutes after placement, indicating that fresh carrion is suitable food for *Nicrophorus*, and that the odor of decay is not the sole attractant for the beetles. In this study, however, silphid beetles did not appear at carcasses until days 3-4. The other major groups of carrion-consumers (Dermestidae, Trogidae) also fall into the category of later colonizers. Hister, dermestid, and trogid beetles appeared at carcasses by days 2-3. In the patterns of immigration surrounding colonization of a carcass, the results of this study suggest that the insects which are most specialized to the necrophagous role are less efficient in initial colonization of carcasses than those forms which utilize carrion in a more opportunistic manner.

An analysis of the efficiency of carcass removal by vertebrate species was calculated by comparing the number of carcasses removed with the total number of carcasses at a site. The combined removal efficiency of coyotes, vultures, and foxes within the first three days of carcass age was approximately 35% at White Sands and 90% at Aden Crater. The removal of carcasses at White Sands
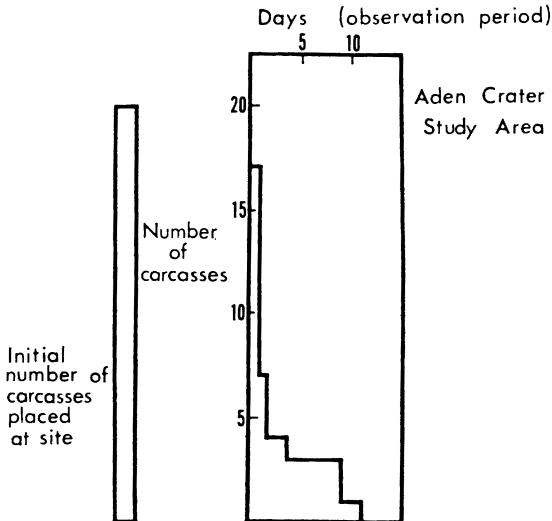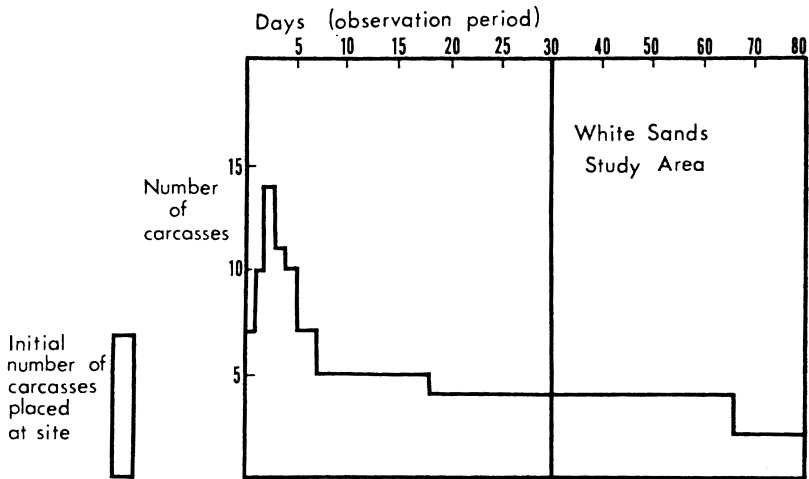
Fig. 5. Numbers of carcasses present at White Sands study area and Aden Crater study area.

and Aden Crater is shown in Fig. 5. The average efficiency on days 1-3 for both sites is approximately 63%. This includes, however, an 11% average removal efficiency for the first day of carcass age. Vultures at Aden Crater also exhibited an approximate 50% efficiency in locating and extensive feeding upon carrion (without removal) within the first day of carcass age. The habit of carcass

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removal by the vertebrate species places the insect populations at a clear disadvantage by eliminating the food source for adults and disrupting the completion of life cycles for any eggs or larvae present in the carcass. The average carcass removal efficiency for the first five days is 73%. Thus it appears that the existence of an insect carrion community such as observed at the site protected from vertebrates occurs less than 30% of the time in the "typical" Chihuahuan Desert habitat when the carcass is small enough to be removed by vertebrate scavengers.

The interpretations of seral stages as presented in this study are valid only for the summer months in which the study was conducted. Considerable seasonal variation in the features of community composition could be expected, as emphasized by Johnson (1975). The peak in insect activity in the Chihuahuan Desert appears to fall during this study period; thus I believe this sampling encompasses most major insect taxa participating in the carcass community. The exceptions are those taxa which are strictly nocturnal, and thus not adequately sampled. The ideal study situation would include constant monitoring by the observer who plans co-habitation with a carcass during the study period. This would produce a more valid sampling, but would eliminate participation by vertebrate species, other than skunks.

Several implications for studies of carcass communities have been realized through this investigation. One of these is certainly the question of evolutionary adaptations by various carrion insects to the competition effected by vertebrate scavengers in the Chihuahuan Desert. It is possible that late colonization by silphid beetles is an adaptation toward insuring that a carcass colonized would be a carcass too large for removal, which would persist long enough to allow completion of the life cycle. If such an adaptation were functional, burying beetles (Nicrophorus) would be unable to perform characteristic movement/burial activities in the optimum breeding situation. Another feature which deserves study is modeling of the energy flow from this community into the general habitat, as might be accomplished through various tissue labeling techniques. Given the scavenger efficiency of vertebrate species, another implication of this study is the possible transmission of parasites to vertebrates through consumption of carrion insects, both adults and larvae.

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