Carrion Reduction by Animals in Contrasting Tropical Habitats

Barney W. Cornaby[1]

Department of Zoology, Brigham Young University, Provo, Utah 84602 U.S.A.

ABSTRACT

Decomposition of lizard (*Iguana iguana, Ctenosaura similis*) and toad (*Bufo marinus*) carrion open to arthropods was studied in a tropical dry and a tropical wet forest in Costa Rica. Carcass fates, feeding interactions of necrophagous animals and their predators, temporal succession patterns, and species compositions differed between sites. More than 170 species representing 49 families were associated with the carrion baits; calliphorid and sarcophagid larvae and adults and adult Formicidae and Scarabaeidae were most important in reducing carcasses to the dry skin stage. The significance of these results is discussed in relation to nutrient cycles and the decomposition submodel of a tropical forest ecosystem.

SYNTHESES OF ENERGY and elemental transfers in tropical forest ecosystems are now available (Golley et al. 1969, McGinnis et al. 1969, Odum and Pigeon 1970, Malaisse et al. 1972, Fittkau and Klinge 1973). The grazing and detritus food chains are the two major pathways for the movement of nutrients in such ecosystems (Odum and de la Cruz 1963, Wiegert and Owen 1971). Nutrients enter the decomposer subsystem via such detritus pathways as annual leaf fall (de la Cruz 1964); total plant death (Richards 1952); seed and fruit drop (Smythe 1970); animal defecation (Watling 1963, Nicholson, Bocock, and Heal 1966); and animal death (Heatwole 1971).

Nutrients tied up in dead animals of various sizes are released in large part by activities of necrophagous bacteria, fungi, and animals. Research on carrion bacteria and fungi is scant (Okafor 1966), but this is not true for investigations of the role of scavenger birds (Chapman 1938, Stager 1964), omnivorous mammals (Koepcke and Koepcke 1952), and arthropods (Chapman and Sankey 1955, Reed 1958). In addition, Fuller (1934), Bornemissza (1957), Payne (1965), and Payne and Crossley (1966) report results of studies on faunas associated with carrion. More specialized research discusses carrion-associated Coleoptera (Pessôa and Lane 1941, Howden 1950, Halffter and Matthews 1966, Shubeck 1969, Payne and King 1969a); Diptera (Hepburn 1943); and Lepidoptera (Payne and King 1969b). These investigations have increased our understanding of the intricate food webs, temporal patterns, and identity of arthropods associated with the carrion microcosm in temperate regions of

the world. Virtually nothing is known about similar phenomena in tropical environments.

The purpose of this research is (1) to document relative durations of the various stages of lizard and toad decomposition in two different tropical forests; (2) to structure preliminary trophic interactions and discuss them in terms of resource partitioning; (3) to detail temporal succession patterns; and (4) to establish an inventory of species attending these carrion. Information about the carrion microcosm will be useful in elucidating detritus compartments of the above-mentioned models of ecosystems.

SITES, MATERIALS AND METHODS

This research was conducted at a tropical dry lowland forest at Finca La Pacifica, 5 km N of Las Cañas, Guanacaste Prov., Costa Rica, and a tropical wet lowland forest 5 km W of Rincón de Osa, Puntarenas Prov., Costa Rica, in the dry season during parts of February and March 1968. From February 8 to February 17 temperatures measured at ground level at the Guanacaste site ranged from 21.8 to 38.5° C with a typical daily fluctuation from 24° C (0400 hr) to 34° C (1300 hr). Ten-year averages of rainfall at Las Cañas (Scott 1966) ranged from a low of 5 mm in January and March, through an average of 17 mm during February to a high of 375 mm in October. In February, the soil was rather dry and loose, and the depth of the dry leaf litter, where existent, averaged 5 cm. The Osa site exhibited temperature extremes of 22.0 and 28.5° C at ground level for the period February 29 to March 9; typical daily fluctuations ranged from 23 to 27° C. Rainfall profile by ten-year averages for nearby Coto, Puntarenas Prov., ranged from 39 mm (February) to 579 mm (October) with 60 mm as the average for March (Scott 1966). The soil was moist, somewhat compact and rocky. Litter depth averaged

4 cm. Minimal selective cutting of large trees had occurred at both forest sites within the last 20 years. Both study areas were at least 200 m from remote human habitations.

Animals native to the respective forests were killed and served as carrion baits: two *Bufo marinus marinus* (Linnaeus) (1 ?, 61 g (wet weights taken immediately after death), 90 mm (snout to vent); 1 ♀, 303 g, 130 mm) and two medium-sized *Ctenosaura similis similis* Gray (♂, 88 g, 145 mm; ♀, 124 g, 168 mm) were studied at Guanacaste; two medium-sized *Iguana iguana iguana* Linnaeus (♂, 261 g, 210 mm; ♂, 291 g, 180 mm) and two *B. m. marinus* (♂, 71 g, 95 mm; ♂, 222 g, 115 mm) were used at Osa. At the sites it was impossible to locate lizard and toads whose sizes exactly matched. Toads were hand retrieved and pithed. Lizards were either noosed and strangled or shot from a tree with a shotgun; there were a few, small perforations in the skin of the latter specimens. Each carcass was placed at the center of a 1 m² square area. The area was cleared of most leaf and twig litter to facilitate observations at the lizard-ground interface as has been done in other carrion studies (Payne 1963, 1965). It was assumed that the carrion fauna was not affected by the partial clearing of such a small area on the forest floor. Individual plots were at least 35 m apart at each site. Carcasses were protected from molestation by vertebrate scavengers by small bottomless wire cages (2 cm x 3 cm mesh size), which permitted large cockroaches and beetles access to the rotting animals.

One lizard and one toad were killed and placed in the field on day one, another pair readied on day four; this staggered placement schedule permitted over 100 hours of observation for the total study and maximized observation time per carcass during the first 3 days of the decay sequence. Numerous observations were made daily at each carcass primarily between 0600 and 1900 hr; several night observations were made also. Each observation lasted from 5 to 180 min with an average of ca. 70 min per observation. The study was conducted at Guanacaste during the following dates in February: 8-15, lizard 1; 11-16, lizard 2; 8-14, toad 1; 11-14, toad 2. Osa dates are as follows: February 29-March 9, lizard 3; March 5-March 12, lizard 4; February 29-March 8, toad 3; March 5-March 12, toad 4. During observation times the cage was lifted away from the carcass. Once placed, carcasses were not moved. The following phenomena were scrutinized at each carrion: decay state of carcass; arrivals, abundances during residency and departures of arthropod taxa; feeding habits by animals on carcass proper and on each

other. One feeding observation represents either the removal of flesh or fluid from the carcass or the capture and ingestion of one organism by a predator(s). Ants and fly larvae ate holes through the body walls of some dead toads and lizards; these breaks permitted observation of the abundances of necrophagous animals inside the carcasses. Activities also were noted as maggots *en masse* undulated under the skin and body walls. Limited voucher specimens of each recognized morpho-species associated with each kind of carcass were collected and labelled daily.

RESULTS

FATE OF CARCASSES: At the dry site (Guanacaste) it was difficult for arthropod reducers to penetrate the thickened integument of the toads. Initial putrefaction was observed up to the second day (24-hr period). However, the carcasses shrivelled and hardened during the next 2 days. Seven days after placement in the field the body-form of the toads was still essentially unaltered and most of the flesh had not been eaten. At Osa, the wet site, the toads were completely stripped of flesh within 5 days. Release of some body liquids, carcass bloating, and partial burial by ants and scarabids were observed during the first 2 days, followed by breakdown of the body by other arthropod reducers during days three through five. By the sixth day only disarticulated bones and dry skin remained.

Dead lizards at Guanacaste were bloated repeatedly during the first 72 hr. Body muscles were being liquified by fly larvae by the third day; the body sagged and the smell of ammonia was noticeable. Most of the flesh had been removed by the reducer organisms within 6 days; however, the muscle tissue of all legs and the tail was never penetrated by dipteran larvae. Even after 10 days these parts remained unconsumed. Breakdown of lizard carrion at the wet site, Osa, was more rapid and more complete. Blood oozings and inflation of the abdomen were observed during the first 24 to 36 hr only. Parts of the carcasses were covered with soil by ant populations during the second and third days; fly larvae penetrated and consumed soft parts of the abdominal and cranial cavities. Ammonia smells were strong. During the fourth and fifth days the muscles of the appendages were eaten so that by day six the decomposition of the lizards was completed except for the bones, cartilage, and some skin. In general, breakdown of carrion was more rapid by one day and more complete at Osa than at Guanacaste. Also, lizard carrion usually required at least one more day to decompose to the dry skin and bones stage than did toad carrion at each site.

FEEDING OBSERVATIONS: Food webs of organisms associated with rotting toads at Osa and Guanacaste (fig. 1) and decaying lizards at the same two sites (fig. 2) are presented. Figures 1 and 2 display not only pathways along which biomass moved but designate relative importances of pathways by the number or width of the connecting lines. The number of observations of detritivores feeding directly on toad fluids and flesh was essentially two orders of magnitude greater on toad carrion at the tropical wet forest than at the tropical dry forest (fig. 1). No feeding observation between predators and possible prey was noted on toads at Guanacaste whereas at Osa there were several interactions. Moreover, a greater diversity of detritivores was associated with the carrion at Osa. Observations of feeding by insect detritivores on lizard carrion were also more numerous at Osa than at Guanacaste (fig. 2). Pathways from carrion to larval and imaginal dipterans were each represented by thousands of feeding interactions at both sites, but formicids were more important at Osa. Predator-prey interactions were three times as numerous at Osa. Ant predation on (a) life stages of dipterans (especially calliphorids, muscids, and sarcophagids), (b) staphylinids, and (c) hymenopterans was more pronounced at Osa than Guanacaste. At the former site staphylinids were important predators on adult flies while at the latter, ant predation on histerids and spider predation on dipterans were especially important. In general, dipterans (especially adult and larval calliphorids, muscids, and sarcophagids), adult formicids, and adult scarabids were the most important detritivores. The most important predators were formicids, frogs and lizards, araneids, and staphylinids.

The number of feeding observations recorded within a site was always greater on the lizard carcasses. As mentioned above, feeding interactions were more numerous at Osa than at Guanacaste for both toad and lizard carrion, respectively. The number of feeding observations follow the pattern: Osa lizards > Guanacaste lizards > Osa toads > Guanacaste toads. The following specific feeding interactions seem especially interesting: the formicid Monacis bispinosus and the scarabid Deltochilum lobipes were of major importance in destruction of the Bufo marinus carrion at Osa. Solenopsis geminata mounded the toad carcass with particles of soil; this activity shielded much of the surface of the toad and appeared to curtail oviposition by dipterans. The calliphorid Phaenicia exima, the sarcophagid Ravinia sp., and the muscid Atherigona orientalis oviposited on lizard carrion and their larvae were apparently important reducers at Guanacaste; the formicid Acromyrmex sp. removed large areas of skin and flesh from lizards at the same site. A population of Pheidole sp. actively mounded the I. iguana with soil. Resolution by species for other feeding observations is possible by inspecting the appendix and matching taxa in figures 1 and 2.
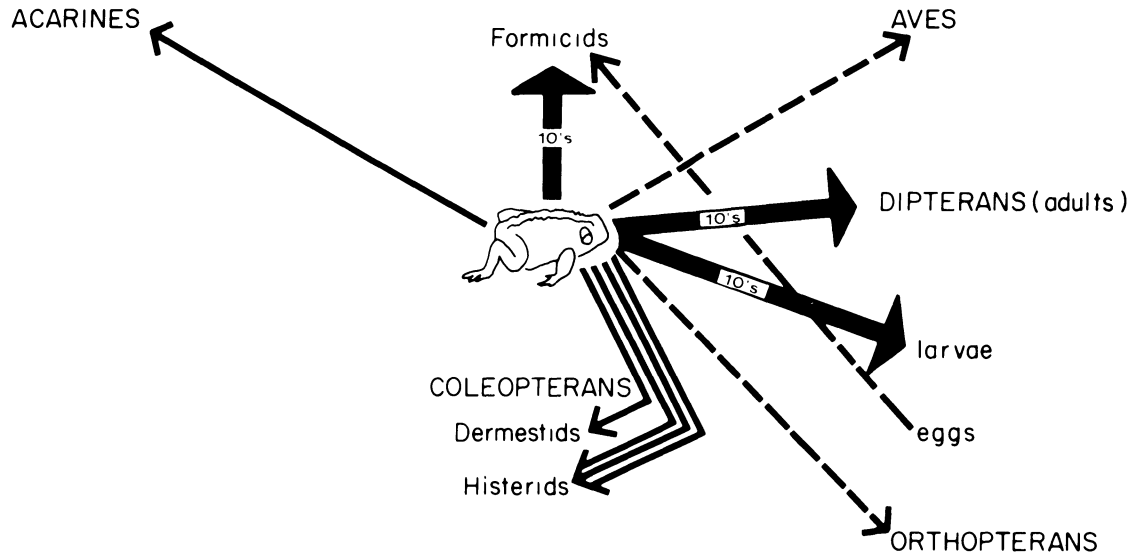
TEMPORAL SUCCESSION PATTERNS: Figure 3 depicts arrival, residence, and departure times for 19 selected families of carrion-associated insects. Also shown are relative abundances of individuals by family through time. Numbers used to generate figure 3 are found in table 1. Only adult and larval calliphorids and sarcophagids and adult formicids remained associated with all carcasses throughout the study. In general, small populations of detritivores arrived first and population recruitment followed. Predators began arriving 1 to 3 days after carcass placement. Populations of both trophic groups peaked on days 3 and 4, then individuals of both groups began leaving the carrion microcosm.

Diel rhythms not evident from figure 3 also existed: populations of adult staphylinids, dipterans, and hymenopterans were lower during the night; in contrast, dictyopteran populations were greater at night.

ARTHROPOD TAXA: The 172 arthropod species collected from the carrion represented at least 49 families and 12 orders. The appendix lists scientific names, forest site and carcass type from which a given species was confirmed. Only three orders accounted for 147 species: Diptera (75), Hymenoptera (42), and Coleoptera (30). Within these, seven families contained 9 or more species per family: Scarabaeidae (11 species); Staphylinidae (10); Muscidae (10) with the dominant genus Fannia comprising 5 of the species; Phoridae (9) with 7 species assigned to the genus Megaselia; Sarcophagidae (9); Sphaeroceridae (10) with Leptocera (6 species) and Sphaerocera (4); and Formicidae (29) with 11 species belonging to the genera, Camponotus (6) and Pheidole (5). The carrion study yielded five new species, four of which were collected at Osa.

Seventeen species were collected and identified from the dead toads at Guanacaste, while 39 species were collected from the toad carrion at the Osa; 2 species were considered in common. Guanacaste lizards yielded 62 species and Osa lizards 103 species with 16 in common. The number of species in common between toad and lizard faunas at Guanacaste was 11 and for a similar comparison with Osa data, it was 22. These patterns were analyzed

TOAD CARRION: TROPICAL DRY FOREST

ACARINES

Formicids
10's

AVES

DIPTERANS (adults)
10's

10's

larvae

eggs

COLEOPTERANS
Dermestids
Histerids

ORTHOPTERANS

TOAD CARRION: TROPICAL WET FOREST

ARANEIDS

ACARINES

DIPLOPODS

Formicids
1000's

SAURIANS

DIPTERANS (adults)

HYMENOPTERANS
(excluding formicids)

100's

1000's

larvae

eggs

COLEOPTERANS
Scarabaeids

Staphylinids

Histerids

ORTHOPTERANS
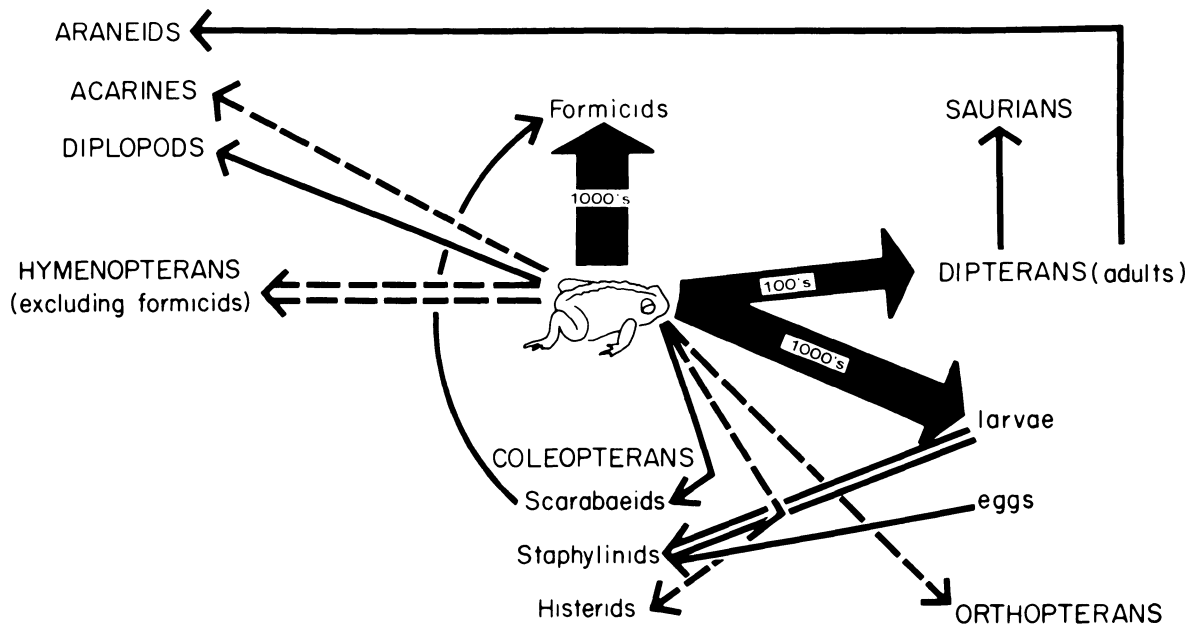
FIGURE 1. Food webs of organisms associated with toad carrion in contrasting tropical habitats. The head of an arrow indicates the direction of the movement of matter and the tail identifies the source. Each normal solid line represents one individual feeding observation. Heavy solid lines show relative numbers of feeding interactions. When a species was repeatedly present on the carcass, but was not seen to feed, the observation of its having fed at another of the carcasses in this study was transferred to the food web as a dotted connectivity.

54   Cornaby

LIZARD CARRION: TROPICAL DRY FOREST

ARANEIDS

ACARINES

Formicids

SAURIANS

100's

HYMENOPTERANS
(excluding formicids)

1000's

DIPTERANS(adults)

1000's

larvae

eggs

LEPIDOPTERANS

COLEOPTERANS

Scarabaeids

Dermestids

Staphylinids

Histerids

ORTHOPTERANS

LIZARD CARRION: TROPICAL WET FOREST

ARANEIDS

SAURIANS

ACARINES

Formicids

ANURANS

1000's

HYMENOPTERANS
(excluding formicids)

1000's

DIPTERANS(adults)

pupae

1000's

larvae

LEPIDOPTERANS

COLEOPTERANS

.15

eggs

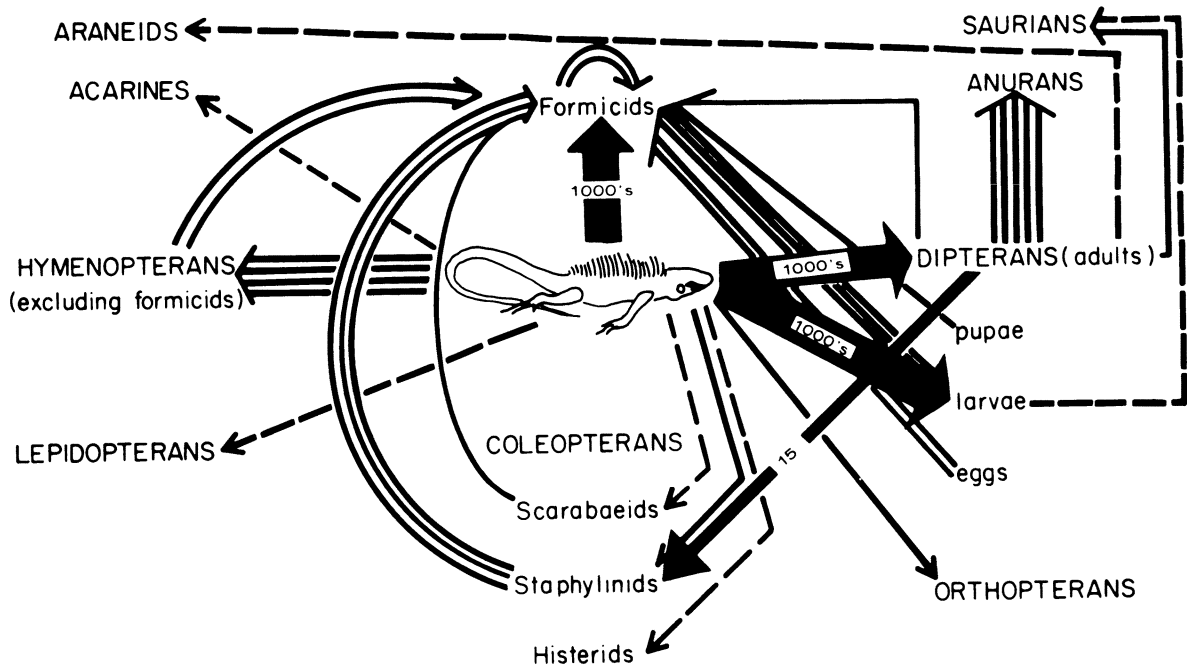Scarabaeids

Staphylinids

Histerids

ORTHOPTERANS

FIGURE 2. Food webs of organisms associated with lizard carrion in contrasting tropical habitats. See legend of figure 1 for explanation.

TABLE 1. *Average numbers of adult individuals associated with carcasses day by day. N = 5–7 counts per day.*

Toads

	Guanacaste 1	2	3	4	5	6	7	Osa 1	2	3	4	5	6	7	8	9
Dictyoptera																
Blattidae	3	1	1								1					
Gryllidae			1					1	1			1	1			
Coleoptera																
Dermestidae		2	2	1												
Histeridae		7	2	11	2				1	2			1			
Scarabaeidae									1	4	2		1	2		
Staphylinidae									3	5	2	1				
Diptera																
Calliphoridae	4	6	2	2	2				1	3	3	1	1			
Chlorophidae																
Drosophilidae	3															
Micropezidae	1															
Muscidae																
Otitidae																
Phoridae																
Sarcophagidae	1	1						1	3	2	1	4				
Sepsidae								1	3	2	2	1				
Sphaeroceridae										1	1					
Hymenoptera																
Apidae																
Formicidae	18	110	200	5	5	5		200	300	275	350	160	22		1	3
Vespidae																
TOTALS	29	137	208	19	9	4		204	317	300	378	172	26	2	1	3

Lizards

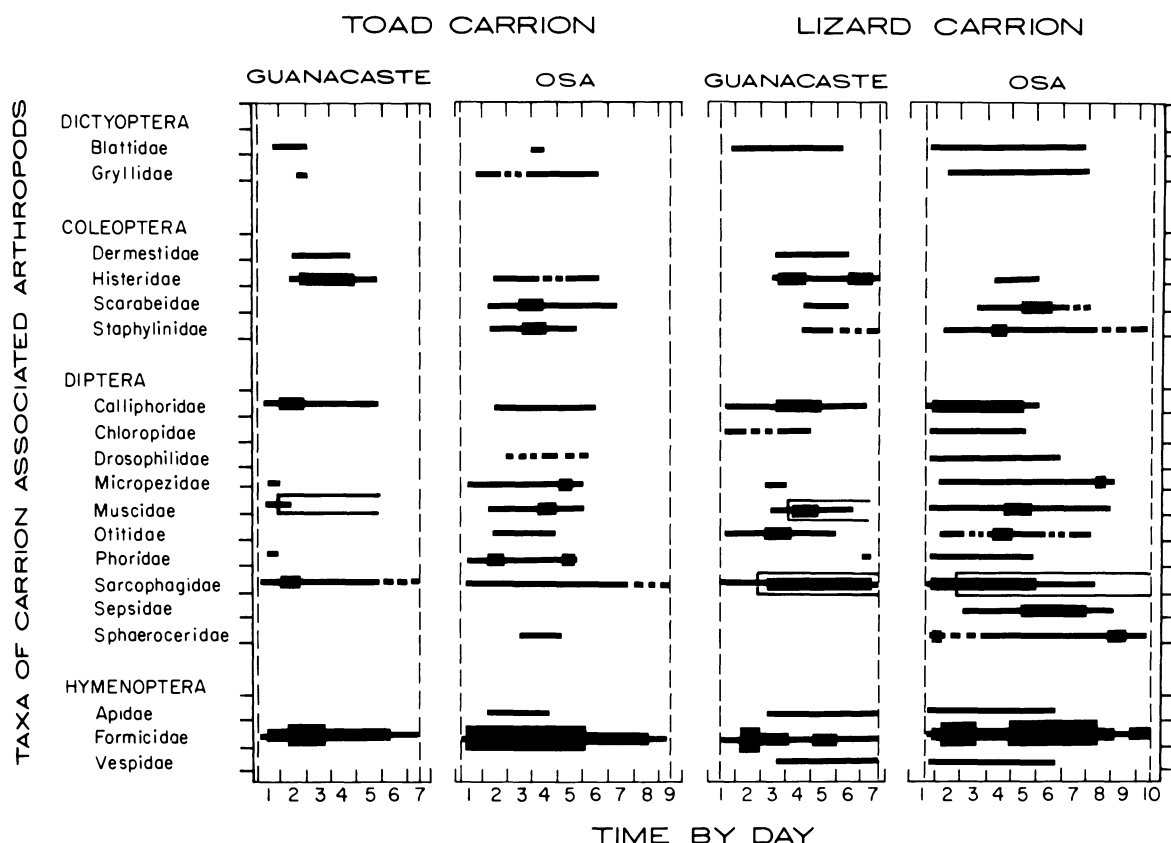|	Guanacaste 1	2	3	4	5	6	7	Osa 1	2	3	4	5	6	7	8	9	10
Dictyoptera																	
Blattidae								2	3	2	1		1	2			2
Gryllidae									1	1		2	4	1			
Coleoptera																	
Dermestidae			3	1	1	2											
Histeridae			5	7	4	5	5				2	4	1				
Scarabaeidae			1	1	1					1	2	6	1				
Staphylinidae			1	1						2	3	3	1	1			2
Diptera																	
Calliphoridae	1	2	19	7	2	2	2	12	11	1	7	5					
Chlorophidae	1		2	2				4	1								
Drosophilidae								1	2	3			2	1			
Micropezidae			2							1	1	2		1	4		
Muscidae			2	11	1	2		1		1	3	4	2	3			
Otitidae	1	3	5	2	3	2				1	8	1		1			
Phoridae										1	1	1					
Sarcophagidae	2	4	15	6	8	6	5	5	4	5	4	8	3				
Sepsidae										3	1	10	16	10	5	1	
Sphaeroceridae			1					1		1	1						
Hymenoptera																	
Apidae			1	1	2	1	3	1	1	1	1	2	1				
Formicidae	3	25	16	3	15	2	1	100	200	300	30	50	100	30	22	5	
Vespidae			2	1	2	2	2	2	2	1	2	2	1				
TOTALS	8	34	72	43	40	25	18	130	229	327	71	101	122	51	36	6	4

56   Cornaby

FIGURE 3. Phenologies of selected families of arthropod reducers associated with toad and lizard in contrasting tropical forests. In each panel the vertical, dotted line to the left indicates time of carcass placement and to the right, time when observations terminated. Populations are indicated with the following scale: ——— = 1-5 individuals; ▬▬ = 6-25; ██████ = 25-100 + adults; ▭▭▭ = 25-100 + larvae. Horizontal dotted lines mean a taxon's presence was suspected, but not confirmed with voucher specimens.

with the following index of similarity (Odum 1971):

$$S = \frac{200\ w}{a + b}$$

where S = percent similarity, w = number of species common to both samples, a = number of species in sample a, and b = number of species in sample b.

Percent similarities for between-site faunas were 7 percent for toads versus toads, 19 percent for lizards versus lizards, and 18 percent for all carrion at Guanacaste versus all carrion at Osa. Finally, within-site faunas for toads versus lizards showed 28 per cent similarity at Guanacaste and 31 percent at Osa.

DISCUSSION

Dead vertebrates occur in various ecosystems around the world. For example, Heatwole (1971) found as many as 1.49 dead Noddy Terns/m² in a transect made on one tropical island. Each summer in the Arctic tundra, there is a flush of thawing lemming carcasses (K. Douce, a tundra biologist, personal communication). Stoddart (1970) placed 45 jackrabbit carcasses in the field to assess scavenging levels by vertebrates in cold deserts and reported that 27 (60%) were eaten by birds but that 18 (40%) were never touched and could have been colonized by necrophagous invertebrates. It can be assumed that input of carcasses to the decomposer subsystem occurs naturally in tropical forests.

Went and Stark (1968) point out that "the bulk of minerals available in the tropical rain forest ecosystem is tied up in dead and living organic systems." Pathways for recycling nutrients from dead components and mechanisms for nutrient retention by the living components may be more numerous in tropical than in temperate forest systems (Witkamp 1970, Odum 1971). Furthermore, nutrient transfers may be more rapid along these pathways

Carrion Reduction in Tropical Habitats   57

than in temperate forests. Although it is difficult to correlate precisely one author's stages of carrion destruction for similar sized organisms with those of another, a general pattern can be deciphered for lowland temperate versus lowland tropical habitats. In North Carolina, U.S.A., Payne (1963, 1965) reported that baby pig carrion open to insects in the summer passed through the flesh, bloated, active decay and advanced decay stages, reaching the dry remains stage in about 8 days. Reed (1958) reported that 10-13 days were necessary in Tennessee, U.S.A., for a similar process in dogs. Rabbits required 9-14 days in Britain (Chapman and Sankey 1955). Bornemissza (1957), working in western Australia with small rodents, indicated that the dry skin stage was recognizable after 40 days. By contrast, in the tropical forest, soft parts of toad and lizard bodies were removed within 5 to 6 days. J. R. Holman (unpublished data) studied carrion of birds, a squirrel and a raccoon at Guanacaste and Osa, Costa Rica, and found that during July and August (the wet season) carrion breakdown was even more accelerated than in the dry season, reaching the dry remains stage in 2½ to 4 days. The size array of carcasses and some of the site characteristics were variable. However, it appears that the process-rate of decomposition for vertebrate carcasses is more rapid in lowland tropical than in lowland temperate forests.

Reed (1958) and Payne (1965) reviewed the vast literature on feeding habits of many carrion-associated arthropod taxa. In general, the observations in the present study are in conformity with their findings. An important distinction appears to be the greater role of ants in the tropics. Reed (1958) and Payne and Crossley (1966) reported 16 species of carrion-associated formicids, whereas I found 29 species. Fuller (1934) found that ants were not of much influence in temperate southern Australia, but at my sites they were important reducers in terms of activity (figs. 1 and 2), abundances (fig. 3), and number of species (Appendix).

Temporal rhythms of the tropical detritivore fauna studied here generally conform to those found by Reed (1958), Bornemissza (1957), and Payne and Crossley (1966) in temperate regions. Many dipterans arrive during the first day after carcass placement, followed on day two through day four by most Coleoptera at the two sites. In Costa Rica formicids tended to arrive sooner and remained in association with carcasses during more of the decay sequences than in North Carolina (Payne 1963, 1965). Although the species of carrion-associated insects from temperate regions differed from those

found in Costa Rica, the ecological equivalents for most temperate taxa were observed and collected in the two Costa Rican forests. These equivalents are represented by such groups as cockroaches, carrion beetles, flesh flies, ants, and bees. Because species structure is more complex in tropical versus temperate communities (Odum 1971), one would expect to measure a greater number of carrion-associated species in the tropical wet forest than in a temperate hardwood forest. The fact that Payne and Crossley (1965) listed 522 carrion-associated species and the present study reports 172 does not invalidate this hypothesis. It is likely that species diversity of tropical carrion faunas would be found to exceed that for temperate faunas if studies as exhaustive as Payne's were to be conducted in tropical rain forests.

One analysis of the data suggests that a particular species-complex of reducer-insects was associated with each kind of vertebrate carcass. The general phenomenon of feeding specificities by insects is well documented, but resource partitioning of certain kinds of vertebrate carcasses by necrophagous insects has not been thoroughly explored. Fuller (1934) noted that dead cats and guinea pigs exposed to similar conditions consistently yielded different species of fly larvae. On the other hand, Hepburn (1943) suggested that apparent differences in species and numbers of dipterans bred from cats, rats, a snake, and a fowl were largely a matter of chance. In another study by Mönnig and Cilliers (1944), 304 carcasses of a variety of vertebrates yielded different assemblages of flies for each type of carcass. Tortoise carcasses, in particular, produced dipteran species different from small mammal carcasses of similar size. Mönnig and Cilliers argued that the best explanation for apparent resource partitionings was a function of size of the carcass. Also, Suenaga (1959) reported that frog carcasses in Japan produced populations of blow fly species different from those of other small animals. It appears, then, that certain dipterans and also other carrion-associated arthropods prefer certain kinds of carcasses, but it is not known if this apparent partitioning of the food resource is a function of size, species, nutrient content, or other condition of the carcass. More exhaustive field work is needed to strengthen the evidence for resource partitioning of vertebrate carcasses by saprophagous arthropods.

Future investigations should concentrate on carrion, rotting fruits, feces, and other detritus as packets of nutrients or energy whose contents are quickly cycled by not only populations of invertebrates, but bacteria and fungi, too. The use of

58   Cornaby

radioisotope tracers can greatly facilitate the mapping of these trophic relationships. Indeed, all aspects of the decomposition processes in tropical forests deserve more attention.

ACKNOWLEDGEMENTS

APPENDIX

Arthropod taxa associated with toad and lizard carrion in two Costa Rican forests during the dry season. The source of voucher is indicated by a letter where A = adult, N = nymph, L = larvae, and J = juvenile; a blank space indicates species was not collected and presumably absent.

Major Taxon	Minor Taxon	Toads		Lizards	
		Guan.	Osa	Guan.	Osa
THYSANURA					
Family indet. (1)	Gen. sp. indet.	A			
COLLEMBOLA					
Entomobryidae (2)	*Drepanocyrtus* sp.		A		
DICTYOPTERA					
Blattidae (*Sensu lato*) (3)	*Euphyllodromia angustata* (Latr.)				N
	Gen. sp. indet.			N	
	Lobodromia sp.			A	
	Neoblattela fraterna (S. & Z.)	N		N	
	Nesomylacris sp. ?				N
	Nyctibora noctivaga Rehn ?				A
Gryllidae (4)	*Nemobius* sp. ?		N		N
	Niquirana sp. ?				N
Tettigoniidae (5)	*Cocconotus* sp.				A
DERMAPTERA					
Carcinophoridae (6)	*Carcinophora americana* (P. de B.)				A,N
HEMIPTERA					
Aradidae (7)	*Proxius palliatus* Champion			A	
Coreidae (8)	*Zicca taeniola* (Dallas)		A		
Gelastocoridae (9)	*Nerthra hungerfordi* Todd			A	
Reduviidae (10)	*Apiomerus* sp. ?			A	
	Rasahus sulcicollis (Serville)				N,A
COLEOPTERA					
Cryptophagidae (11)	*Toramus lentus* Sharp				A
Cucujidae (12)	*Ahasverus* near *rectus* (LeConte)			A	
Dermestidae (13)	*Dermestes carnivorus* F.	A		A	
Histeridae (14)	*Euspilotus* (*Neosaprinus*) sp.		A	A	A
	E. (*N.*) sp.	A		A	
Leptodiridae (15)	*Dissochaetus* sp.		A		A
Nitidulidae (16)	*Stelidota strigosa* (Gyll.)			A	

Carrion Reduction in Tropical Habitats   59

Family	Species					
Scarabaeidae (17)	*Anaides* near *plana* Chapin, n. sp.			A		
	Canthon lamprimum Bates				A	
	Coilodes castanea Westwood			A		A
	Deltochilum lobipes Bates			A		A
	D. sp.				A	
	Eurysternus caribaeus (Hbst.)			A		
	E. claudicans Kirsch			A		
	E. plebejus Harold			A		A
	E. n. sp. ?					A
	Onthophagus acuminatus Harold					A
	O. praecellens Bates			A		
Staphylinidae (18)	Gen. sp. 1			A		A
	Gen. sp. 2					A
	Gen. sp. 3				A	
	Gen. sp. 4					A
	Gen. sp. 5					A
	Gen. sp. 6			A		
	Gen. sp. 7			A		A
	Gen. sp. 8					A
	Gen. sp. 9				A	
	Gen. sp. 10			A	A	A
Tenebrionidae (19)	*Blapstinus tibialis* Champion				A	
	B. sp.				A	
DIPTERA						
Calliphoridae (20)	*Chloroprocta fuscianipennis* (Macq.)					A
	Cochliomyia macellaria (F.)				A	
	Hemilucilia flavifacies (Engel)			A		
	H. segmentaria (F.)					A
	Mesembrinella sp.				A	A
	Phaenicia eximia (Weid.)	A			A	A
Chloropidae (21)	*Conioscinella* sp.				A	
	Hippelates pusio Lw.				A	
	H. near *dissidens* (Tuck.)				A	
	Oscinella longipalpus End.?					A
	Siphonella prosthiomelas End.					A
Dolichopodidae (22)	*Chrysotus* sp.			A		
	Condylostylus sp.					A
Drosophilidae (23)	*Drosphila* sp. 1					A
	D. sp. 2					A
	Mycodrosophila sp. 1					A
	M. sp. 2					A
	Zygothrica sp.					A
Micropezidae (24)	*Plocoscelus arthriticus* (Wiedmann)			A		A
	P. niger (Schiner)					A
	Taeniaptera albibasis (Enderlein)					A
	T. grata (Wulp)				A	
	T. planitibia (Enderlein)					A
	T. near *albibasis*					A
Milichiidae (25)	*Meoneura* sp.				A	
Muscidae (26)	*Atherigona orientalis* Sch.		L		A	
	Cyrtoneurina conspersa (Stein)			A		A
	C. gemina (Weid.)			A	A	A
	C. mimica Snyder					A
	Graphomyia sp.			A		A
	Fannia sp. 1			A		A
	F. sp. 2			A	A	A
	F. sp. 3					A
	F. sp. 4					A
	Pseudoptilolepis nigripoda Snyder					A
Neriidae (27)	*Glyphidops flavifrons* (Bigot)			A		A
Otitidae (28)	*Acrosticta apicalis* (Williston)				A	
	Euxesta schineri Hendel				A	
	E. near *annonae* Fabricius			A		A
	E. near *maculata* Hendel				A	
	Notogramma cimiciforme Loew				A	
Phoridae (29)	*Dohrniphora* sp.					A
	Megaselia sp. 1			A		A
	M. sp. 2				A	A
	M. sp. 3					A
	M. sp. 4					A
	M. sp. 5					A
	M. sp. 6		A			

	Species	1	2	3	4
	M. sp. 7		A		
	Puliciphora sp.				A
Piophilidae (30)	Protopiophila n. sp.				A
Prixoscelididae (31)	Trixoscelis n. sp. near mohavea Melander			A	
Richardiidae (32)	Epiplatea hondurana Steyskal	A			
Sarcophagidae (33)	Eumacronychia sternalis Allen	A		A	
	Helicobia rapax (Walker)	A			
	Oxysarcodexia sp.			A	
	Paraphrissopoda sp.			A	
	Ravinia sp.			A	
	Peckia sp.			A	
	Sarcodexia sternodontis Twnsnd.				A
	Sarcophaga sp. (sensu lato)			L,A	L,A
	Tricharaea sp.			A	
Sepsidae (34)	Meropliosepsis sexsetosa Duda				A
	Palaeosepsis armata (Schiner)				A
	P. n. sp. ?				A
Sphaeroceridae (35)	Leptocera (Bromeloecia) bromeliarum (Knab and Malloch)				A
	Leptocera (Pterogramma) sp. 1				A
	L. (P.) sp. 2		A		
	L. (P.) sp. 3		A		
	L. (P.) sp. 4				A
	L. (P.) sp. 5				A
	Sphaerocera (Parasphaerocera) sp. 1		A		A
	S. (P.) sp. 2		A		
	S. (P.) sp. 3				A
	S. (P.) sp. 4				A

HYMENOPTERA

	Species	1	2	3	4
Apidae (36)	Trigona (Trigona) amalthea (Olivier)				A
	T. (Hypotrigona) atomaria (Cockerell)				A
	T. (Plebeia) frontalis Friese				A
	T. (Trigona) fulviventris fulviventris Guerin-Meneville			A	A
	T. (Paratrigona) opaca Cockerell				A
	T. (Trigona) ruficrus corvina Cockerell				A
	T. trinidadensis silvestriana Vachel			A	A
Braconidae (37)	Heterospilus sp.		A		
Chalcididae (38)	Brachymeria fonscolombei (Dufour)			A	
Cynipidae (30)	Trissodontaspis sp.				A
Diapriidae (40)	Spilomicrus sp.			A	
Formicidae (41)					
(Dolichoderinae)	Monacis bispinosus (Olivier)		A		A
(Formicinae)	Camponotus (Myrmothrix) abdominalis (F.)			A	
	C. (Myrmocladoecus) rectangularis Emery	A		A	
	C. (Myrmepomis) sericeiventris (Guerin)			A	A
	C. (Tanaemyrmex) sp. 1				A
	C. (T.) sp. 2			A	
	C. (T.) sp. 3				
(Myrmicinae)	Acromyrmex sp.			A	A
	Aphaenogaster sp.				A
	Monomorium carbonarium ebeninum Forel	A	A		
	Oligomyrmex sp.				A
	Paracryptocerus sp.			A	
	Pheidole sp. 1				A
	P. sp. 2			A	A
	P. sp. 3	A			
	P. sp. 4			A	
	P. sp. 5	A			
	Solenopsis geminata (F.)		A		A
(Ponerinae)	Ectatomma ruidum Roger	A		A	A
	E. tuberculatum (Olivier)			A	
	E. sp. near edentatum Roger				A
	Gnamptogenys haenschi Emery				A
	G. striatula (Emery)			A	A
	G. tornata (Roger)				A
	Neoponera apicalis (Latreille)				A
	Odontomachus haematodus (L.)	A		A	
	Pachycondyla sp.		A		
(Pseudomyrmicinae)	Pseudomyrmex sp. 1	A		A	
	P. sp. 2				A
Vespidae (42)	Stelopolybia areata (Say)			A	A
	S. panamensis (Cam.)?				A

ARANAE

Clubionidae? (43)	Gen. sp. indet.				A
Ctenidae (44)	*Ctenus falcatus* Pickard-Cambridge				A
	Ctenus sp.				J
Salticidae (45)	*Phiale simplicicava* (Cambridge)			A	

ACARI

Families indet. (46)	Gen. sp. indet.	A	A	A	A

OPILIONES

Phalangodidae (47)	*Pachylicus rugosus* Banks				A

ISOPODA

Family indet. (48)	Gen. sp. indet.			A	

DIPLOPODA

Spriostreptidae (49)	*Orthoroporus* sp.				A

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