

Decomposition Patterns in Terrestrial and Intertidal Habitats on Oahu Island and Coconut Island, Hawaii

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ABSTRACT: Decomposition studies were conducted at two sites on the Island of Oahu, Hawaii, to compare patterns of decomposition and arthropod invasion in intertidal and adjacent terrestrial habitats. The animal model used was the domestic pig. One site was on Coconut Island in Kaneohe Bay on the northeast side of Oahu, and the second was conducted in an anchialine pool located at Barber's Point Naval Air Station on the southwest shore of Oahu. At both sites, the terrestrial animal decomposed in a manner similar to what has been observed in previous studies in terrestrial habitats on the island of Oahu. Rate of biomass depletion was slower in both intertidal studies, and decomposition was primarily due to tide and wave activity and bacterial decomposition. No permanent colonization of carcasses by insects was seen for the intertidal carcass at Coconut Island. At the anchialine pool at Barber's Point Naval Air Station, Diptera larvae were responsible for biomass removal until the carcass was reduced below the water line and, from that point on, bacterial action was the means of decomposition. Marine and terrestrial scavengers were present at both sites although their impact on decomposition was negligible. Five stages of decomposition were recognized for the intertidal sites: fresh, buoyant/floating, deterioration/disintegration, buoyant remains, and scattered skeletal.

KEYWORDS: forensic science, forensic pathology, forensic entomology, decomposition, marine, postmortem interval, tropical

A decomposing body discovered in the intertidal habitat presents investigators with a series of unique challenges to estimate the postmortem interval. Several studies have been conducted documenting the differences that exist between marine and terrestrial environments in decomposition patterns (1). In a marine environment, there are many factors affecting decomposition that are not encountered in terrestrial habitats. These include salinity, depth, water currents, nature of substrate, as well as the numbers and kinds of scavenging organisms present (2). Most decomposition studies conducted in either terrestrial or marine habitats have been in temperate environments, and relatively few studies have been conducted in either environment in tropical habitats (3). There are significant differences between temperate and tropical situations (3), related to temperature, rainfall, and vegetation. While there have been various studies on patterns of decomposition in terres-

trial and marine environments (4–7), little is known about decomposition and ecology of carrion in the intertidal zone. This ecotone is an interface between marine and terrestrial habitats and carrion-associated taxa are a combination of scavengers and colonizers from both habitats (8,9). The present study provides preliminary data on succession and physical changes to the decomposing body to assist in estimations of postmortem intervals in the intertidal habitat.

This study seeks to: (1) identify the recognizable stages of decomposition for carrion in the intertidal ecotone in a tropical habitat; (2) compare the rate of biomass removal in intertidal and terrestrial habitats; (3) document the diversity and characteristics of carrion-associate taxa in intertidal habitats; and (4) note the influence of tidal fluctuations and currents on decomposition.

Materials and Methods

Study Sites

This study was conducted at two sites on the island of Oahu, Hawaii: Coconut Island, and Barber's Point Naval Air Station.

Coconut Island is located in the middle of Kaneohe Bay on the windward coast of the island of Oahu (157°47'28"W 21°26'22"N). The island is approximately 320 m away from the shore of Oahu and is approximately 500 m long by 200 m wide. The waters surrounding the island constitute a recognized marine preserve. The island is owned and operated by the University of Hawaii. The Hawaii Institute of Marine Biology occupies most of the island and maintains laboratories, a fleet of small boats, accommodations, and administrative offices. A total of 20 people live on the island and approximately 100 people commute to work on the island on a daily basis. Public access to the island is restricted and access is only by boat.

The study site was located on the northern shore of the island, approximately 220 m from the island's outer reef wave break. This site receives tidal wash and trade winds from the Northern Pacific Ocean. The site was completely exposed to the sun. Salinity of surrounding waters during the study period was measured with an AGE Salinometer Model 2100 as 35.3 ppt, with some variation due to rainfall. Ground consisted primarily of smooth pebbles/rocks (5 to 10 cm in diameter), broken coral on the surface, and a sand substrate with a sparse covering of grassy vegetation. Scattered debris from ocean and land sources washed up along the study site. Vegetation surrounding the site consisted primarily of coconut palms (*Cocos mucifera*). Few vertebrates live on the island: rats (*Rattus rattus*), mice (*Mus musculus*), one cat (*Felis silvestris f. catus*), and birds.

¹ Graduate research assistant and professor of entomology, respectively, Department of Entomology, University of Hawaii at Manoa, Honolulu, HI 96822.

*Current address: 714th Medical Detachment, Fort Bragg, NC 28307-5000.
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Barber's Point Naval Air Station is located on the southern coastline (leeward coast) of the island of Oahu. The area is owned and operated by the Federal Government with the U.S. Coast Guard and U.S. Navy maintaining airfields, an air station, family accommodations, shopping facilities, and administrative offices, all accessible by car. Approximately 5400 people live and work in the area, although public access is restricted.

The study site (158°03'17" W, 21°18'37"N) is an anchialine pool ("brackish pond") as defined by Brock and Bailey-Brock (10). In this sense, an anchialine pool is "a land-locked brackish body of water that undergoes tidal fluctuations, but lacks surface connections to the sea." The pool is approximately 700 m from the white sand beach bordering the station and is approximately 100 m in diameter and 6 to 7 m deep. The study site was completely exposed to the sun. Salinity during the study period (Jan. 1998 to Apr. 1998) was measured using an AGE Salinometer Model 2100 and found to be 19.4 ppt. Connection with the ocean was through the porous underground substrate, believed to be limestone. Range of tidal movement during the study period was measured using a vertical 2 m scale embedded in the pond's shore and was found to be 5 to 8 cm. These tidal fluctuations are not visibly obvious without the scale. Soil was fine with a high organic content. Ground cover consisted of small shrubs and plants (*Pluchea indica*, *Pluchea symphytifolia*, *Heliotropium curassavicum*, *Leuceana leucocephala*, *Sesuvium portulacastrum*), red mangroves (*Rhizophora mangle*), and cheave trees (*Prosopis juliflora*). A population of the small Indian mongoose (*Herpestes auro-punctatus*) is present and active in the area.

Animal Model

The animal model for this study was the domestic pig, *Sus scrofa* L., as this most closely approximates the pattern of human decomposition (11,12). Recommended size for study animals is approximately 23 kg (12); however, work by Hewadikaram and Goff (13) demonstrated that some variation in carcass size did not significantly influence patterns of decomposition or taxa present. Carcasses were provided by the University of Hawaii Experimental Farm, Haleiwa. Two carcasses were used for each study, with two repetitions at each site, for a total of eight carcasses. For the first replication at the Coconut Island site and the second replication at the Barber's Point site, carcasses were chilled, but not frozen, prior to being placed at the sites. The remaining animals were freshly killed and not chilled prior to being placed at the sites. Carcasses were held in sealed double plastic bags between death and placement at the sites to prevent insect activity prior to field exposure.

Procedures

Two studies each were conducted at the Coconut Island and Barber's Point sites. Each study was continued for a period of 42 days or until decomposition ceased. The Coconut Island studies were conducted from 13 Aug. to 22 Aug. 1997 (10 days) and 18 Sept. to 29 Oct. 1997 (42 days). The Barber's Point studies were conducted from 8 Jan. to 7 Feb. 1998 (31 days) and 21 Mar. to 27 Apr. 1998 (38 days).

During each study, the intertidal carcass was placed between the high and low tide marks for each site. This ensured that there was contact between the carcass and seawater during the high tide, simulating a body "washed up on shore." The terrestrial carcass was placed no less than 25 m from the intertidal carcass at each site. Substrate was similar for these carcasses, but above the high tide

mark, and the carcass was not in contact with seawater. Carcasses were placed on their backs on a welded wire mesh (5 × 10 cm) weight platform (1.0 × 0.5 m), reinforced with wooden dowels. An enclosure cage (1.0 × 1.0 × 0.5 m) of the same welded wire mesh was placed over each carcass to prevent vertebrate depredation. A Whitmire PT[®] 24 Yellow Monitoring Card was attached to the top of each cage, directly over the carcass. Another Whitmire PT[®] yellow monitoring card was placed approximately 25 m away from the study site in order to determine which insects were attracted to the carcasses and which just to the monitoring card.

For the first three days of each study, carcasses were examined every 2 h. Following that, carcasses were examined twice a day until the end of the study. At each visit, surface and internal temperatures of the mouth, abdomen, and anus were recorded, along with ambient air and substrate temperatures. Relative humidity and wind velocity were recorded. A hygrothermograph at each site provided continuous records of ambient relative humidity and temperatures. Once each day, maximum/minimum ambient air temperatures were recorded and rainfall measured using a rain gauge at the site. Weight of each animal was taken using a handheld scale to determine the rate of biomass removal. Soil samples were taken at each site prior to beginning the studies to establish the normal soil fauna and pH was taken. Soil samples were taken every third day for the duration of each study. For the first Coconut Island study, soil samples were processed following a marine sampling technique following Sanders et al. (14). Samples from other studies were processed in a Berlese funnel, as this technique proved more effective in extracting organisms from the soil.

At each visit, observations were made and recorded of the stage of decomposition and organisms on and around each carcass. Representative samples were taken of all taxa seen on the carcasses. Samples of immature forms were split into two parts. One part was killed and fixed in KAA (15) and later transferred to 70% ETOH for preservation. The remaining immatures were reared in the laboratory to the adult stage for species identification. Adult insects were killed and preserved in 70% ETOH or dried and pinned, as appropriate for taxa involved. Marine organisms were preserved in 10% formalin. After the insect succession began to slow, frequency of collection was reduced to once per day.

Results and Discussion

Stages of Decomposition

Terrestrial—Four recognizable stages of decomposition were observed for all terrestrial carcasses at both sites. These stages conform to the Goff (12) terrestrial model: fresh, bloated, decay, and post-decay. The fifth stage in this model, skeletal, was not reached by any of the carcasses before the study ended. This may have resulted from several factors: (1) premature hardening of the skin making the carcass unattractive to flies more rapidly than normal (16); (2) the rapid transition to the post-decay stage, precluding extensive activities by skin-feeding taxa; (3) possible effects of salt spray from adjacent marine habitats; and (4) time constraints of the study. Other terrestrial studies on the island of Oahu have reached the skeletal stage in 42 days (1,13,17). If the carcasses in the present study had remained in place longer, the skeletal stage would have been attained.

Intertidal—The stages of decomposition observed in the intertidal ecotone represent a hybrid of the aquatic model described by Payne and King (5), and the terrestrial models described by Early

and Goff (18) and Goff (12). The stages were not completely distinct but may be generally characterized as follows:

1. *Fresh*—This stage begins at the moment of death and continues until bloating is first observed. Carcasses at both sites were placed on the substrate but remained partially exposed during this stage and were never completely submerged, even during high tide. Weight increased shortly following placement as the carcasses took on water through the natural body openings. Adult Diptera (predominantly Calliphoridae and Sarcophagidae) were immediately attracted to the carcasses and began to deposit eggs or larvae. Carcasses showed a greenish-black discoloration of the abdomen as the stage progressed.

2. *Buoyant/Floating*—This stage began as the carcasses began to bloat, due to the gases being produced by the activities of anaerobic bacteria in the abdomen. The Coconut Island carcasses floated for limited periods of time when the tide was high enough to raise the carcass. At the Barber's Point site, the carcasses did not float since marginal tidal fluctuations did not result in an increase sufficient to raise the carcasses. Stronger odors of decomposition were evident at the Barber's Point site due to limited water circulation.

3. *Deterioration/Disintegration*—During this stage, skin began to disintegrate and easily flake off or break away. Skin became stringy on the outer portions of the body. Fatty tissues separated from the body and floated on the surface of the water. A film of oil was observed on the surface in the vicinity of the carcasses. This stage was much shorter at the Coconut Island site because of the wave action that caused rapid disarticulation and soft tissue removal.

4. *Buoyant Remains*—During this stage, parts of the bones, skin, and tissue still remained partially suspended under the water, with some elements partially exposed. Bones were separated from tissues and an oil slick was present near the carcasses. Marine fauna avoided stagnant areas with poor water circulation. Pieces of skin, tissue, and fat floated in the vicinity of the carcass. With increased water action, fatty tissues were scattered along the shoreline and adhered to rocks.

5. *Scattered Skeletal*—This stage had the same appearance at both sites. No skin or soft tissues remained, only fat and bones. These remains settled to the bottom and were scattered by under-water currents and wave action. Scattering was more wide at Coconut Island due to the more exposed nature of the site to wave and current actions.

In comparing the results of the present study with those from Payne and King (1972), it must be kept in mind that none of the carcasses in this study were ever completely submerged. Between the two sites, differences were noted in rates of decomposition and patterns of biomass removal.

Biomass Removal

Terrestrial—As shown in Figs. 1 and 2, biomass removal was more rapid for terrestrial carcasses than for those in the intertidal area. This difference was primarily due to greater, sustained arthropod activity on terrestrial carcasses. This rapid removal of biomass continued until approximately 10 to 20% of the biomass remained. At this point, the skin had hardened and was unsuitable for maggot feeding and the rate of removal decreased.

Intertidal—As shown in Figs. 1 and 2, the rate of biomass removal was slower for intertidal carcasses than for terrestrial at each

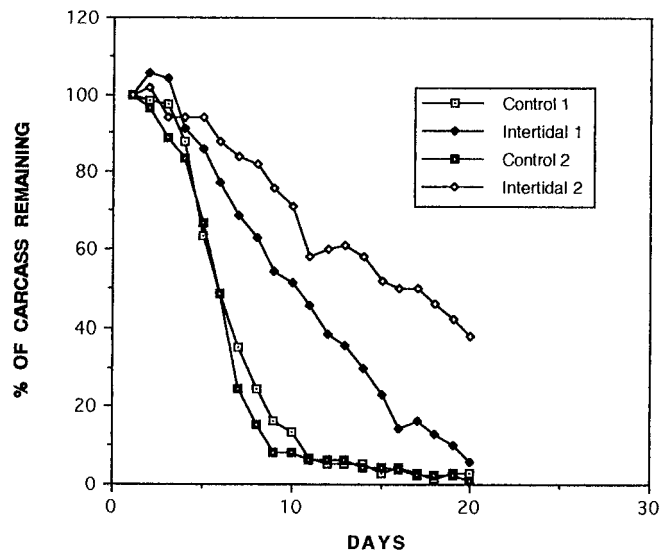


FIG. 1—Rates of biomass removal over time from intertidal and control carcasses at Barber's Point Naval Air Station expressed as percent weight remaining.

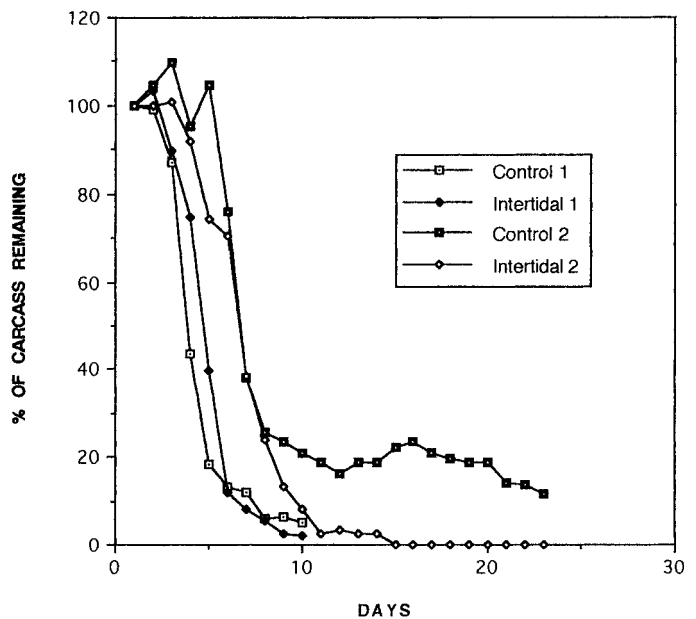


FIG. 2—Rates of biomass removal over time from intertidal and control carcasses at Coconut Island site expressed as percent weight remaining.

site. The rate of breakdown of the intertidal carcasses was more rapid at the Coconut Island site than at the Barber's Point site. While differences in salinity between the two sites may have impacted on the decomposition processes, wave action and currents were major factors assisting in decomposition at the Coconut Island site. Here, arthropod succession did not occur because the waves washed off most eggs within hours of being laid. Waves and currents ripped apart the carcasses, preventing permanent colonization by maggots, and also resulting in rapid loss of biomass. Soft tissue removal began at the joints, flexible regions, and extremities, followed by the main torso. Approximately 80% of the total biomass was removed within the first 4 to 7 days. The fifth

stage, scattered skeletal, was reached within 10 days during the first, and within 15 days in the second replication. Had the carcasses not been secured to the platform inside an enclosure cage, but allowed to move freely with the waves and tides, it is likely that disarticulation and disintegration would have occurred even more rapidly.

At the Barber's Point site in the anchialine pond, arthropods (primarily Diptera) were the major decomposers. Tidal fluctuations at this site were minimal and most of the carcass was continually exposed above the waterline. At no time during this study were the carcasses completely covered by water. As in studies by Payne and King (1972), maggots were the primary initial invaders, removing flesh above the water line. Within the first 15 to 18 days, maggots removed approximately 80% of the exposed biomass, but were unable to exploit the food resources below the water line. Because these carcasses were placed on their backs, maggots never penetrated the submerged portions of the head and anus. Approximately 30 to 50% of the carcass remained following cessation of maggots activity. After this, biomass removal was the result of bacterial activity and marine fauna (e.g., fish and crabs). During the first study at the Barber's Point site, it took 23 days for the remaining portions of the carcass to be reduced to the fifth stage and 38 days for the second. In contrast to the terrestrial situation, carcass reduction was a gradual decrease.

Faunal Diversity and Characteristics

Table 1 shows the organisms associated with the decomposing carcasses at the Coconut Island and Barber's Point sites. A total of 109 species were recovered from both sites, representing 82

families and 8 phyla. Of these species, 75% were arthropods. The species associated with the terrestrial carcasses were more diverse at the Barber's Point site than at Coconut Island. Necrophagous arthropods were the primary decomposers of terrestrial carcasses. Predatory beetles in the families Histeridae and Staphylinidae, skin-feeding beetles in the Dermestidae and Cleridae, and isopods were present at the Barber's Point site but noticeably absent from the Coconut Island site. The Diptera present at the Coconut Island site were also less diverse than noted for the Barber's Point site. This apparent lack of diversity may be attributed in part to the geographical separation of Coconut Island from the main island of Oahu. The taxa and numbers reported from the Coconut Island site were similar to what had been previously noted for decomposing bodies found on boats moored offshore on Oahu (Goff, personal observations). Ants were also a significant factor in reducing the fly eggs and maggots found on terrestrial carcasses at the Barber's Point site but not on Coconut Island. Initial predation by ants at this site may have delayed the initial onset of biomass removal, as was noted by Early and Goff (18) in previous studies on Oahu. The lack of parasites and predators at the Coconut Island site allowed for greater maggot activity and a resulting rate of initial biomass removal that was greater than for the Barber's Point site.

In spite of the proximity of the terrestrial carcasses to water, no marine taxa were observed on terrestrial carcasses at either site. At the Coconut Island site, crabs and fish were associated with the intertidal carcasses, but had no apparent impact on the rate of biomass removal. As was also the situation noted by Lord and Burger (19), crabs were observed feeding on soft tissues and larvae on the carcasses. At the Barber's Point site, fish and aquatic arthro-

TABLE 1—Classified list of taxa collected from decomposition studies at Coconut Island and Barber's Point Naval Air Station, Oahu, Hawaii.

Phylum	Class	Order	Family	Genus and Species	Coconut Island		Barber's Point	
					1*	T†	I	T
Cnidaria	Anthozoa	Madreporaria	Zoanthidae	<i>Palythoa vestitus</i>	X			
Platyhelminthes	Turbellaria	Acoela		<i>Convoluta</i> spp.	X			
Nemertea				spp	X			
Nematoda				sp A	X			
Sipuncula				<i>Siphonosoima rotumanum</i>	X			
Mollusca	Gastropoda	Prosobranchia	Trochidae	<i>Trochus intextus</i>	X			
			Melanidae	sp A	X			
			Neritidae	<i>Nerita picea</i>	X			
Annelida	Cephalopoda	Dibranchiata	Polypodidae	<i>Octopus cyanea</i>	X			
	Oligochaeta			sp A	X	X		
	Polychaeta	Errantia	Syllidae	<i>Syllinae</i> spp	X			
				<i>Typosyllus aciculata</i>	X			
				<i>orientalis</i>				
				<i>Brania mediodentata</i>	X			
				<i>Pionosyllus</i> spp	X			
				<i>Sphaerosyllus</i> spp	X			
Arthropoda	Chelicerata	Araneae	Salticidae	spp	X	X	X	X
		Pseudoscorpionida		sp		X		
	Acari	Parasitiformes		Gamasida (immatures)		X		X
			Macrochelidae			X		X
			Uropodidae			X		X
		Acariformes		Oribatida spp		X		X
	Crustacea	Copepoda		sp A	X			
	Malacostraca	Stomatopoda	Squillidae	<i>Pseudosquilla ciliata</i>	X			
		Amphipoda	Gammaridae	sp A	X	X	X	
		Isopoda	Cirolanidae	<i>Cirolana</i> spp		X		

(continues)

TABLE 1—Continued.

Phylum	Class	Order	Family	Genus and Species	Coconut Island		Barber's Point		
					I*	T†	I	T	
		Decapoda	Ligidae	<i>Ligia</i> spp		X		X	
			Portunidae	<i>Thalamita crenata</i>	X				
			Grapsidae		<i>Metapograpsus messor</i>	X			
					<i>Grapsus tenuicrustatus</i>	X			
			Porcellanidae		sp A	X			
		Paguridae		<i>Calcinus latens</i>	X				
				<i>Clibanarius zebra</i>	X				
	Chilopoda		Scolopendridae	<i>Scolopendra subspinipes</i>		X		X	
	Hexapoda	Collembola	Sminthuridae	sp A				X	
				Onychiruridae	sp A				X
		Thysanura	Lepismatidae	immatures				X	
	Orthoptera	Gryllidae		sp A	X	X	X	X	
			Blattaria	Blattellidae					X
		Blaberidae						X	
	Dermaptera	Labiiduridae						X	
				Labiidae					X
	Psocoptera		Liposcelidae	<i>Liposcelis</i> sp				X	
	Hemiptera		Gerridae				X		
			Cydnidae	sp A		X		X	
			Anthocoridae	sp A				X	
	Homoptera		Aphidae					X	
	Thysanoptera		Phlaeothripidae			X		X	
			Thripidae				X	X	
	Coleoptera	Cleridae		<i>Necrobia rufipes</i>		X		X	
				<i>Necrobia ruficollis</i>				X	X
		Dermestidae		<i>Dermestes ater</i>			X	X	
				<i>Dermestes frischii</i>				X	
			<i>Dermestes maculatus</i>				X	X	
		Histeridae		<i>Saprinus lugens</i>				X	
				<i>Atholus rothkirchi</i>				X	
		Staphylinidae		<i>Philonthus longicornis</i>			X	X	
		Tenebrionidae	sp A					X	
		Scarabaeidae	sp A					X	
		Ptilidae	sp A			X		X	
		Anobiidae	sp A			X		X	
		Bostrichidae	sp A					X	
		Coccinellidae	sp A					X	
		Hydrophilidae	sp A				X		
		Elateridae	sp A				X	X	
	Diptera	Calliphoridae		<i>Chrysomya megaphala</i>	X	X	X	X	
				<i>Chrysomya ruficacies</i>	X	X	X	X	X
		Sarcophagidae		<i>Phaenicia cuprina</i>	X	X	X	X	
				spp (larvae)	X	X	X	X	
			<i>Boettcherisca peregrina</i>	X	X	X	X		
			<i>Parasarcophaga ruficonis</i>	X	X	X	X		
		Muscidae		<i>Fannia pusio</i>		X	X	X	
				<i>Ophyra chalcogaster</i>	X	X	X	X	
			<i>Ophyra aenescens</i>				X	X	
			<i>Musca domestica</i>	X	X	X	X	X	
			<i>Gymnodia</i> spp				X	X	
			<i>Physiphora</i> spp				X	X	
		Drosophilidae	sp A		X	X	X	X	
		Sciaridae	sp A			X		X	
		Scenopinidae	larvae					X	
		Dolichopodidae	sp A		X	X	X	X	
		Chloropidae	sp A		X	X	X	X	
		Milichiidae	<i>Milichiella lacteipennis</i>	X	X	X	X	X	
		Bombyliidae	sp A				X		
		Tephretidae	sp A		X	X			
		Psychodidae	sp A			X		X	
		Cecidomyiidae	sp A				X	X	
		Syrphidae	<i>Eristalis arvorum</i>				X		
		Ephydriidae	<i>Discomyza maculipennis</i>	X	X	X	X	X	

TABLE 1—Continued.

Phylum	Class	Order	Family	Genus and Species	Coconut Island		Barber's Point				
					1*	T†	I	T			
Chordata			Hymenoptera	Formicidae	<i>Monomorium minutum</i>	X	X	X	X		
					<i>Solenopsis geminata</i>	X	X	X	X		
				Sphecidae	<i>Pison insulare</i>			X	X		
					<i>Ectimneus polynesialis</i>			X	X		
					<i>Brachymeria fonscolombei</i>			X	X		
				Eulopidae	sp A		X		X		
				Evaniiidae	<i>Evania appendigaster</i>			X	X		
				Apidae	<i>Apis mellifera</i>			X			
				Vespidae	sp A			X			
				Mammalia	Carnivora	Viveridae	<i>Herpestes auropunctatus</i>				X
				Reptilia	Squamata	Iguanidae	<i>Anolis carolinensis</i>				X
						Gekkonidae	<i>Lepidodactylus lugubris</i>				X
				Aves	Passeriformes		<i>Paroaria coronata</i>				X
							<i>Acridotheres tristis</i>		X		
				Chondrichthes	Galeomorpha	Sphyrnidae	<i>Sphyrna lewini</i>	X			
				Osteichthyes			<i>Gambusia affinis</i>				X
							<i>Poecilia latipinna</i>				X
						Acanthuridae	<i>Acanthurus triostegus</i>	X			
			Pomacentridae	<i>Abudefduf abdominalis</i>	X						
			Muraenidae	<i>Gymnothorax</i> spp	X						
			Blenniidae	<i>Bathygobius fuscus</i>	X						

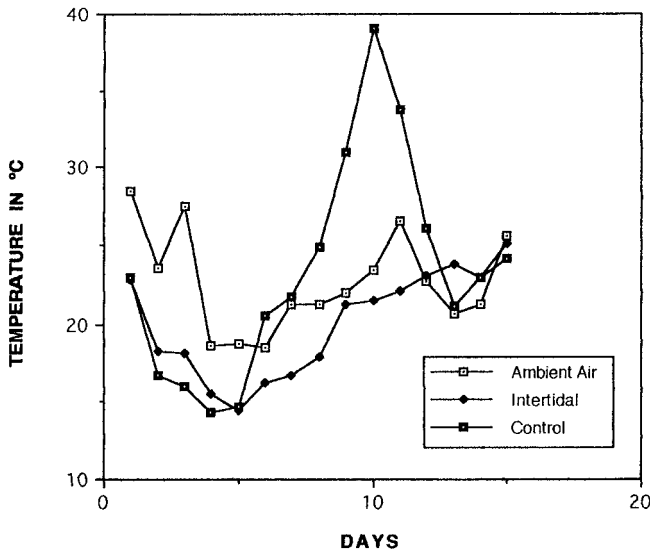


FIG. 3—Ambient temperatures and internal carcass temperatures for control and intertidal carcasses at the Barber's Point Naval Air Station.

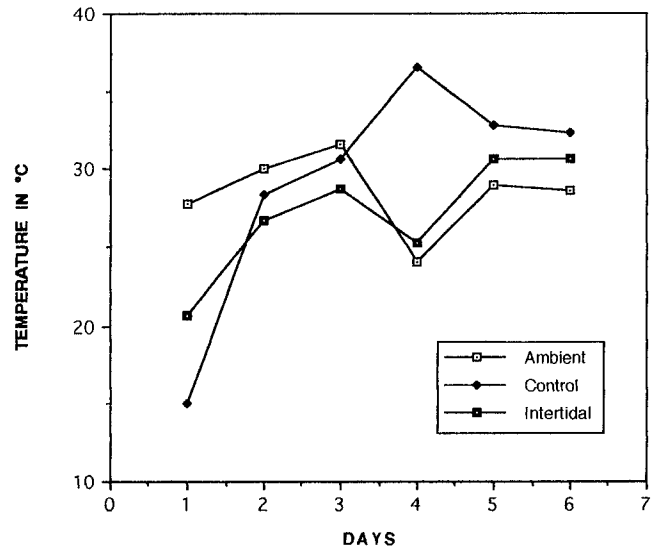


FIG. 4—Ambient temperatures and internal carcass temperatures for control and intertidal carcasses at the Coconut Island site.

Pods were seen feeding on the soft tissues and larvae, but with no apparent effect.

Water is a key factor in the differences between intertidal and terrestrial decomposition (16). The presence of water limits access of arthropod necrophages to the carcass (5) as well as promoting bacterial activity. In the intertidal carcasses, the flesh remained soft and pliable throughout the studies, while the skin hardened in the terrestrial carcasses. The constant action of the waves on the carcass at the Coconut Island site resulted in disarticulation of the carcasses and increased the rate of biomass removal. Variation in tidal levels appeared to have a minimal impact on the process, although

currents were responsible for dispersal of bones along the shoreline during the last stage of decomposition.

Water was a mediating factor in the carcass temperatures, as well as arthropod colonization. Initially, internal body temperatures of all carcasses were similar to the ambient air temperatures at each site. In the terrestrial carcasses, once maggots began feeding, internal temperatures of the formed maggot mass exceeded ambient air temperatures (Figs. 3 and 4). These increased temperatures occurred first in the head, associated with natural body openings providing initial sites for arthropod invasion, followed by the anus. As maggot masses migrated toward the abdomen, abdominal temper-

atures rose, while those in the head and anus returned to near ambient. This is similar to patterns observed in other terrestrial decomposition studies (3,18).

There was considerable difference between temperature patterns in the terrestrial and intertidal carcasses. The internal temperatures of the intertidal carcasses approximated those of the surrounding water. Where maggot masses were formed, the mass temperatures rose above the daily maximum ambient air temperatures. However, those temperatures were not as high as those produced by the larger masses formed on terrestrial carcasses.

Conclusions

This study demonstrated clear differences between the decomposition of carcasses in terrestrial and intertidal habitats. The pattern of decomposition and the organisms found on the carcasses varied according to habitat, temperature, and degree of exposure to water. Patterns of decomposition in the intertidal and terrestrial habitats in this study were compared with previously published studies. Terrestrial decomposition at both sites was consistent with the model proposed by Goff (12). Results of intertidal studies exhibited a number of differences from the model proposed by Payne and King (5).

The complete carrion community was more diverse and larger on the terrestrial carcasses compared to the intertidal carcasses. Adult flies were equally attracted to both terrestrial and intertidal carcasses at both study sites. Colonization was limited by water for the intertidal carcasses, but terrestrial carcasses showed normal levels of colonization. Colonization by flies was accomplished above the water line at the Barber's Point site, but not at Coconut Island.

The pattern of decomposition in the intertidal habitat is impacted by the same factors that affect decomposition in a marine habitat: temperature, salinity, depth, currents, nature of substrate, and number and kind of scavenging organisms (2). However, unlike results of previous studies (1,2,20), the primary decomposers of remains were not fish, mollusks, crustaceans, or echinoderms. In the intertidal habitat, Diptera during the early stages of decomposition and bacterial activity combined with the physical factors of wave action, tides, and water currents were the primary factors in decomposition. Dipteran activity was limited by the degree of access allowed by the carcass placement.

Tidal fluctuations greatly influenced the decomposition of carcasses in the intertidal ecotone. Carrion communities were directly impacted by exposure to currents, waves, tidal changes, and water depth. With greater exposure to wave action and deeper water, there was less oviposition by adult flies, lower levels of maggot activity, and lower internal carcass temperatures. While intertidal decomposition was characterized by an initially slow rate of biomass removal, wave and current action ensured the complete disposition of the carcasses. Less wave action and tidal fluctuations, as at the Barber's Point site, resulted in slower rates of disarticulation and decomposition.

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Additional information and reprint requests:

M. Lee Goff,
Department of Entomology
University of Hawaii at Manoa,
Honolulu, HI 96822