male and four female mesenteries alternating in pairs of like sex. Each female mesentery contained between two and five oocytes, but more usually three, which formed a string along the oral-aboral axis just behind the mesenterial filament. In contrast the oocytes of *Favites mathaii* formed clusters at the aboral end of each mesentery and there were between 200 and 500 oocytes per polyp, depending on polyp size. These oocytes were smaller than those of *Acropora* spp. (Table 1).

Most species investigated contained oocytes and testes in the same polyp. The exceptions to simultaneous hermaphroditism appeared to be the species *Porites lutea* and *Fungia fungites* in which only either testes or oocytes were detected.

In many species of coral which have external fertilization, testes develop rapidly and oocytes often become colored in the final stages of maturation (Kojis and Quinn, 1981; Harrison *et. al.*, 1984). The most dramatic changes in the appearance of the gonads occur during the month prior to spawning (Harrison, pers. comm.). Although no data are presented here regarding the mode of reproduction, this study indicates that many species are in the latter stages of a gametogenic cycle. Coloring of the oocytes is mostly associated with more mature testes. However not all species are equally mature (Table 1). It is likely that most of the species considered here will spawn in the summer or early fall and that different species will spawn at different times. Indeed, a survey of *Acropora valida* and *Acropora irregularis* in early September (Paul Gates, pers. comm.) indicated that both species had already spawned.

In Australia (Harrison *et al.*, 1984), the Red Sea (Loya, pers. comm.) and Hawaii (Krupp, 1983) spawning occurs about the time of either the new or full moon. Abe (1937) reported that *Goniastrea aspera* spawned at the time of the new moon in October–November at Palau. No species were observed to spawn in Guam around the full moon in June. Future investigation of reproduction in Guam corals would be most profitable during July, August and September. Long term studies are required to determine whether gametogenesis is annual or more frequent and to what degree populations around the island are synchronized.

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FOOD PREFERENCES AND FEEDING BEHAVIOR OF THE LAND CRAB *Cardisoma carnifex*

ABSTRACT—Observations were made of food preferences and feeding behavior of *Cardisoma carnifex*, a common Pacific land crab. The major portion of the diet of these crabs is made up of detritus, but they also eat leaves, fruits, and seeds of some plant species.

These crabs serve as local seed dispersal agents for certain preferred plant species by their habit of carrying the fruit away from where they discover it, and discarding the seeds after consuming the fruit. For other plant species *C. carnifex* acts as a seed and seedling predator.

Introduction

Cardisoma carnifex (Herbst.) is a common land crab widely distributed throughout the Indo-Pacific region. Adult crabs are 8–13 cm in carapace width; chelipeds are unequal, conspicuously so in males (Bliss, 1968; Yaldwyn and Wodzicki, 1979). Females deposit fertilized eggs in the ocean and juveniles return to land when quite small and remain terrestrial (Bliss, 1968). *C. carnifex* usually live in burrows dug down to ground water, but also utilize crevices such as the bases of trees as shelters (Powers and Bliss, 1983). Like other land crabs, they are opportunistic scavengers consuming a wide variety of organic material.

It has been suggested that *Cardisoma carnifex* plays a number of important roles in the communities it inhabits. Several researchers have observed that *C. carnifex* may influence vegetation patterns by acting as a seed disperser and as a seed predator. In a study on Bimini, Howard (1950) observed that land crabs (species not identified) transported seeds from the beach into interior areas and often abandoned them. In investigating several crab burrows he noted apparently undamaged seeds stored there. He suggests that land crabs may be aiding in the establishment of some plant species by moving seeds to sites favorable to germination and growth. Alexander (1979) observed *C. carnifex* on Aldabra, an atoll in the Indian Ocean. He notes that through seed predation crabs may be important in controlling plant numbers.

Here I report some preliminary observations on the food preferences and feeding behavior of *Cardisoma carnifex* and suggest how these crabs may influence vegetation patterns. This study was done on Fanning Island, also known as Tabuaeran Island. This is a small atoll which is part of the Line Island chain, and is located about 1000 nautical miles south of Hawaii. The flora of Fanning I. has been described by St. John (1973). Some general observations on *Cardisoma carnifex* on this island are provided by Fellows et al. (1973).

Methods

The purpose of this research was to investigate the potential role of *Cardisoma carnifex* as a seed predator and a seed disperser. In particular I sought to determine what plant species might be most affected by these crabs. The diet of these crabs and their feeding behavior was assessed through observations in three different habitats, a mixed forest on the lagoon shore, an open coconut woodland with a grass and herbaceous ground cover, and a grove of *Calophyllum inophyllum* (Guttiferae). A total of 6 hours was spent in observation in each habitat. Note was taken of what the crabs were eating, and their behavior in searching for and consuming food. These data exclude the observations made in the course of the experiments reported below.

Food preference experiments were carried out in the mixed forest using three species common in this habitat; *Scaevola taccada* (Goodeniaceae), *Tournefortia argentea* (Boraginaceae), and *Pandanus tectorius* (Pandanaceae). I placed fruits of these species in areas of high crab activity and observed from several meters away. The fruits used varied greatly in size, for example *Pandanus* fruits may be 8–10 cm in length, but the fruits of *Tournefortia* and *Scaevola* are considerably smaller. *Scaevola* drupes are circular with a diameter of about 1 cm; and *Tournefortia* fruit is about half that size. To help avoid whatever biases might be introduced by this difference in fruit size, I used large numbers of small fruits placed in a pile, and single large fruits. Note was taken of the way the crabs located the bait, the fruit chosen by the crab, and the activity of the crabs once the bait was taken. Crabs were considered to have used sensory cues to locate the fruit if they changed their initial direction of movement and approached the bait directly from a distance of at least .5m. Fifteen replicates were done with all three species, and an additional ten replicates with only *Scaevola taccada* and *Tournefortia argentea*.

In this study, *C. carnifex* was found to be a seed predator of only one plant species, *Calophyllum inophyllum*. I performed a simple experiment to investigate the extent of this predation. Eight regularly placed quadrats (1 × 3 m) were established in a small grove of *C. inophyllum*. The quadrats were cleared of sprouting seeds, then one marked sprouting seed was placed in each. This density is equal to the density of sprouting seeds found when clearing these plots. Quadrats were checked every 24h and missing seeds replaced. The experiment continued for 6 days. In addition, the total number of seedlings, the number of seedlings apparently damaged by crabs, and the number of crab burrows were determined for each quadrat.

Results

Both detritus and living organic matter, such as fruit and leaves, are important food items for *Cardisoma carnifex* (Table 1). Detritus is apparently the more common; however fruits, leaves and seeds make up a significant portion of the food of these crabs. The fruit of *Pandanus tectorius* appears to be a frequent food item.

An important aspect of the feeding behavior of these crabs is the preferences they exhibit for fruit of certain species. The fruits of all three species tested are eaten by crabs, but clear preferences are shown (Table 2). *Pandanus tectorius* is preferred over *Scaevola frutescens* and *Tournefortia argentea*. When *Pandanus* is not present, *Scaevola* is preferred over *Tournefortia*.

In most cases (92%) crabs carried the food item away before eating it. This is probably to avoid competition from other crabs (Herreid, 1963). Both *Pandanus* and *Scaevola* produce drupaceous fruit, that is they have a fleshy exocarp and a hard endocarp surrounding the seed. The crabs eat the fleshy portions but discard the seeds. This, together with the habit of moving the fruit before consuming it combine to make *Cardisoma carnifex* a potentially important agent of local dispersal for these species. *Tournefortia* produces a small dry fruit that is apparently not very appealing to *C. carnifex,* and it seems likely that these crabs do not have an important role as seed dispersers in this species.

Food searching behavior was observed in the three habitats. Sensory cues are apparently important to *Cardisoma carnifex* in finding food. In 44% of the food preference experiments crabs were judged to have located the fruit by such cues, although whether vision or smell was involved cannot be determined. In the remainder of the cases crabs located the fruit through random scavenging. Herreid (1963) reports that *C. guanhumi* use both vision and auditory senses (hearing fruit fall) in finding food. I did not test for auditory cues. These crabs do not seem to locate food by the presence of other individuals, unlike *Coenobita* spp. (hermit crabs) (Kurta, 1982), and in general *C. carnifex* feeds alone. Only one instance of group feeding was observed. This was the case of an open coconut which had several *C. carnifex* and a number of *Coenobita* spp. feeding at it.

To some extent food searching behavior seems related to habitat. In the forest on Fanning Island, crabs are constantly moving and scavenging and seem to travel considerable distances in their search for food. This habitat lacks an herbaceous understory because of the heavy shade, and the litter layer is not thick or continuous due to rapid decomposition. Thus crabs are probably forced to search more extensively for food. The forest borders on the lagoon and many crabs sit in the shallows of the lagoon and eat detritus they pick from the sandy bottom. Individual crabs were observed to travel up to 40m through the forest to reach the lagoon shore. In a more open habitat of coconut trees with extensive undergrowth of grass and herbs, crabs travel less and spend considerable time just outside their burrows eàting the leaves of herbaceous plants.

The possibility of *C. carnifex* storing uneaten seeds in burrows, and thus providing a suitable habitat for germination, is problematic. In the forest, crabs do not usually live in burrows and when they find a food item they simply carry it to a sheltered area, such as a

Table 1. Observations on Food Items of *Cardisoma carnifex*

Type of food	*Number (and percent) of observations*
dead organic matter	57 (63%)
living organic matter	33 (37%)
Food Item—living organic matter	*Number of observations*
Pandanus fruit	12
Calophyllum seed	4
Scaevola fruit	1
Pisonia leaves	2
Leaves of grass and forbs (spp. unidentified)	7
Unidentified fruit	7

Table 2. Food Preference of *Cardisoma carnifex*

Fruits Presented	Number of Replicates	Number of Times Fruit Selected First			No Preference[a]	Fruit carried away	Fruit eaten in place
		Pandanus	*Scaevola*	*Tournefortia*			
Pandanus, Scaevola, and *Tournefortia*	15	12		1	2	15	0
Scaevola and *Tournefortia*	10	—	9		1	8	2

[a] no preference shown—crab took all bait

Table 3. *Cardisoma carnifex* impacts on *Calophyllum inophyllum*

Total number of seedlings	94
Mean number/quadrat	11.75
Average seedling density (m^2)	1.3
Average crab burrow density (m^2)	1.2
Number of seedlings damaged	79
Percent seedlings damaged	84%

fallen log. In other habitats, such as the open coconut woodland or the *Calophyllum inophyllum* grove, where crabs do live in burrows, individuals were observed taking uneaten fruit into their holes, but many simply carried it away from other crabs before beginning to eat. Crabs periodically clean and re-excavate their burrows, so it seems unlikely that stored seeds would be in holes long enough to germinate. However, no burrows were investigated in this study and further work on this point is obviously needed.

For only one plant species was *C. carnifex* observed to be a seed predator. This is *Calophyllum inophyllum,* a large Indo-Pacific tree common in coastal habitats. *Calophyllum* produces a round drupe about 3–4 cm thick. The endocarp is dry and thin, and apparently is not eaten by the crabs. The seeds, however are popular food items. Crabs were observed investigating these drupes but were never seen cracking the shell, rather they chose drupes which had begun to sprout. When the seed sprouts, one end of the shell cracks allowing the root to emerge, and this opening gives the crabs access to the seed. Forty percent of the marked sprouting seeds were taken by crabs over the period of the experiment. On a daily basis, removal rates ranged between 25% and 63%. This appears low, considering the high density of crabs living in the area, and the effect of this predation is not clearly evident (Table 3). Numerous seedlings are present, indicating reproduction is high. However, many of these seedlings are damaged, apparently due to crabs. Crabs were seen feeding on leaves of *Calophyllum* seedlings. They grab the edge of the leaf blade and pull. Sometimes the complete leaf is removed; at other times this results in the removal of a large rectangular portion of the blade. Based on these observations, seedlings were judged to be damaged by crabs if they were defoliated or if leaves were missing pieces in the characteristic rectangular pattern. Of the seedlings counted, 84% exhibited such damage. This ranged from complete defoliation to partial damage to one or two leaves only. As *Cardisoma* was the only species of land crab observed in this habitat it is likely that it has an important impact on reproduction of *Calophyllum* since it eats both the seeds and the seedlings.

Conclusion

This study indicates that *Cardisoma carnifex* plays two quite different roles in the plant ecology of the communities it inhabits. For some plant species, these crabs serve as local dispersal agents, for others they act as seed and seedling predators. As *C. carnifex* inhabits strand areas where vertebrate seed dispersers are usually lacking, they may be of particular importance to the plant species involved. The effect of seed and seedling predation by these crabs is unclear. In the one example found in this study, *Calophyllum inophyllum,* predation rates on both seeds and seedlings were significant, but the overall impact on reproduction was not determined. Obviously more research is needed. It is clear that the food preferences and feeding behavior of *Cardisoma carnifex* have the potential for making this crab an important factor in the reproduction of certain plant species. Future research will investigate the extent of this impact.

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The Vegetation and Anthropogenic Disturbance of Toloa Forest, Tongatapu Island, South Pacific

Tropical forests in general are being threatened by the activities of humans (Myers 1980). Tropical insular forests are no exceptions (Wodzicki 1981). There is a need to describe such forests threatened with destruction as well as a need to describe the nature and extent of the anthropogenic disturbance regime. Here I briefly discuss the vegetation and anthropogenic disturbance of Toloa Forest, Tongatapu Island, the Kingdom of Tonga, South Pacific.

Tongatapu is approximately 3500 km NE of Sydney, Australia, has an area of 250 km, and a maximum elevation of around 90 m. The average annual temperature is 23.3 C and the annual rainfall is 172.8 cm (Crane 1979). Toloa forest has negligible slope, an elevation of around 50 m, and an area of approximately 20ha, and is located near the end of a runway at Fua'amoto Airport. The forest is managed by Tupou College. There is only one other inland forest which is comparable in size, but it is dominated almost exclusively by *Aleurites moluccana,* an aboriginally introduced species.

In December 1981, a total of 50 circular 100 m^2 quadrats were randomly located along seven NW-SE transect lines. Within each quadrat, trees (defined as woody nonvine plants with a diameter at breast height greater than 10 cm), large saplings (individuals of tree species with a diameter between 2.5 and 10 cm), small saplings (individuals of tree species with a diameter less than 2.5 cm), seedlings (individuals of tree species shorter than breast height), and lianas (woody vines) were sampled. Dominance for trees is here calculated from basal area, and dominance for seedlings is calculated from Braun-Blanquet cover estimates converted into percentages (Mueller-Dombois and Ellenberg 1974). Density was determined for trees and saplings, and frequency (percent of plots occupied) was determined for all categories of woody plants. For each category, importance values were calculated by averaging relative dominance, relative density, and relative frequency, or whichever of these were available.

The importance values for trees, large and small saplings, seedlings, and lianas are shown in Table 1. *Rhus taitensis* and *Elattostachys falcata* are the most important trees. The understory trees *Vavaea amicorum* and *Syzigium clusiifolium* are the most important species in the seedling and sapling categories. *Dioscorea bulbifera* and *Jasminum simplicifolium* are the most frequent lianas. Toloa Forest is similar to the *Alphitonia-Rhus* association described by Straatmans (1964) and the *Rhus* secondary forest described by Whistler (1980) in that all three have *Rhus taitensis* and *Alphitonia zizyphoides* as important canopy species. Straatmans (1964) describes how the *Elattostachys falcata-Callophyllum vitiense* association gradually replaces the *Alphitonia-Rhus* association on 'Eua Island. In Toloa Forest, *Elattostachys falcata* and *Elaeocarpus tonganus* are likely to increase in importance because of their high representation in the smaller size classes (Table 1). *Rhus taitensis,* with almost no representation in small size classes, will eventually disappear, or perhaps become established only in large canopy gaps (Whistler 1980).

Because Toloa Forest is the last non-coastal natural wooded area on Tongatapu, it serves as a refuge for many of the island's native species. The red shining parrot, *Prosopeia tabuensis tabuensis,* actually named for the island of Tongatapu, is considered extinct on the island by Watling (1982). However, there is a small population in Toloa Forest. Plant species which