Ecology of the Coconut Rhinoceros Beetle, *Oryctes rhinoceros* (L.) (Coleoptera: Dynastidae)[1]

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ABSTRACT

The Coconut Rhinoceros Beetle (*Oryctes rhinoceros*) is a major pest of the coconut palm in its Asian homeland and on the South Pacific islands it has invaded. Each adult female lays 3 or 4 clutches, with about 30 eggs per clutch, in logs or other concentrations of organic material over a period of 9 to 12 weeks. Eggs incubate 11 days, and, under favorable conditions, the first feeding of the adult will occur 17 weeks later. Boring down into the folded, emerging fronds, the adult can damage spadices and leaflets, with consequent loss in coconut production. The palm dies if the growing tip is destroyed by the beetle or by secondary infections. In hard logs or other nutritionally poor sites, pre-adult mortality of beetles may exceed 98 percent. However, many sites created by typhoons or human activities are more favorable and contribute to beetle population increase. To prevent economic losses, it is necessary to identify and remove or destroy these beetle-producing sites.

DURING THE PERIOD between March 1964 and July 1967, I was employed as Ecologist (Project Area) with the U.N.-S.P.C. Coconut Rhinoceros Beetle Project. Most of my research was done on the island of Upolu in Western Samoa but I also visited Tutuila, American Samoa; Tongatapu and Vavau, Tonga; Viti Levu, Fiji; Nukunono in the Tokelaus; and several islands in the Palaus. My final contribution to the Project was a survey, made during May and June 1967, of coconut and other palm areas in Malaysia, Thailand, and the Philippines.

In all these locations, throughout its Asian homeland (India to Indonesia) and on the South Pacific islands it has invaded since 1909, *Oryctes rhinoceros* (L.) is closely associated with the coconut palm, *Cocos nucifera* L. The adult beetle chews down into the folded, emerging fronds of a coconut palm, pushing out fiber and feeding on cell exudations. The immature stages are commonly found in coconut logs or stumps, although they can also occur in sawdust heaps and almost any other concentration of organic material. Despite its close links with the coconut palm, *O. rhinoceros* may have evolved in association with another palm. Paine (1967) suggested it might have subsisted primarily on inland palms, such as *Corypha* spp., which die after flowering. Under such circumstances, the availability of oviposition sites and larval food would not depend on palm mortality caused by adult feeding or other extrinsic factors. Whatever its original host may have been, *O. rhinoceros* was well adapted to utilize palm plantations.

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Gressitt (1953), Cumber (1957), and Paine (1967) have all emphasized the correlation between abundance of larval food and damage by adults to palms. The Rhinoceros Beetle is most apt to be of economic importance whenever and wherever coconut logs or other sites suitable for larval feeding are numerous. Either natural catastrophes or human destruction can create outbreak foci. Examples include:

1. Typhoons—These are most important in Samoa, Tonga, Fiji, and the Palaus and less so elsewhere, even on the east coast of Luzon.
2. Diseases—"Cadang-Cadang" virus has led to extensive palm mortality on Luzon. There is an interesting possibility that the Rhinoceros Beetle may serve as its vector.
3. Senility—Palms dying of old age are common in parts of Western Samoa and the Philippines.
4. Replanting—This, of course, overlaps the previous category, but it also includes the expansion of oil palm plantations into former rubber estates in Malaysia (Wood 1968), and planting in zones cleared of jungle. Any time logs or stumps are left in or near an area replanted to palms, the Rhinoceros Beetle can increase.
5. Milling—Sawmills provide larval food throughout the range of *O. rhinoceros*. Other sites occur near palm oil and sago mills in Malaysia and coir factories in the Philippines.
6. Composting—Piles of grass, rice straw, and manure, if large enough, provide another type of outbreak focus.
7. Military Devastation—This final category was quite important in the Palaus (Gressitt 1953) and may now be important in Viet Nam.

Cumber (1957) rightly indicated that any type of outbreak focus can expand and become self-perpetuating if attacks by the adult beetles become frequent enough to kill mature palms. This situation has happened on Koror and Peleliu in the Palaus and along the inland margins of plantations in Western Samoa.

My previous publications on the Rhinoceros Beetle described the damage it does to Pacific Island palms (Hinckley 1966) and animals associated with adults or immature stages in Western Samoa (Hinckley 1967). This paper presents an ecological life history of the beetle, describing some of the behavioral and environmental factors that determine the location, number, and survival of each stage from egg through imago. Such information can help in the prediction of outbreaks and the identification of dangerously productive sites.

For descriptions of the Samoan environment, see Buxton and Hopkins (1927), Fox and Cumberland (1962), Kennedy (1968), and Wright (1963).

TECHNIQUES

Field techniques included: direct collection of adults from palms and of all stages from ground sites; trapping of adults at light and in artificial stumps; and exposure of standard (one meter long) coconut logs in different habitats. In the insectary and laboratory, observations were made on flight, oviposition, incubation, larval development, and adult feeding.

The collections of beetles from palms were usually made along transects through plantations. Each fresh burrow was probed with a hooked wire. If a beetle was present, it was removed, then taken back to the laboratory where it was measured and either dissected or used in behavior studies. The depths of occupied and empty burrows were measured. This procedure provided some information on feeding which was supplemented by laboratory trials with beetles in palm petioles or sugar cane.

Other beetles were caught in artificial stump traps. These traps (fig. 1) were made, in their simplest form, of three parts: a 1.8 m coconut log base embedded upright 30 cm in the ground, a tin can 11 cm deep and 15 cm wide placed on the log, and, on top of the tin, a 30 cm high coconut log cap, centrally perforated by a hole 2.5 cm wide. The diameters of the caps and bases were usually between 16 and 24 cm. At night, beetles landed on the cap, crawled down the hole and fell in the tin. The bases of the traps had to be replaced annually and the caps changed every six months. However, it was possible to use the old caps for oviposition trials, confining a female beetle in a cap, then splitting the cap, making an egg count, and wiring the cap together again for further use.

FIGURE 1. Artificial tree stump at Nafanua Agricultural Experiment Station, W. Samoa, in June 1966. (Note beetle-damaged palms in background.)

For field collections from logs, heaps, and other breeding sites, measurements were made of volume, density, moisture content, and pH. All stages of *O. rhinoceros* were counted and the presence of mortality or competitive factors noted.

Similar records were kept for the meter-long coconut logs exposed during the periods between August 1965 and April 1967 in Western Samoa and between April 1966 and May 1967 in Malaysia (set up by Mr. C. R. Wallace). In both countries, some of the logs were partially concealed by ground cover or low canopies and others were out in open fields surrounded by short grass. The objective of these trials was to evaluate the effects of "vegetative barriers" on the discovery and utilization of logs by the Rhinoceros Beetle or competitive organisms (other beetles, termites, etc.).

OBSERVATIONS

LIFE CYCLE.—In table 1, the life cycle of *Oryctes rhinoceros* is summarized. These estimates are based on observations made in Western Samoa, but they agree closely with those made by Gressitt (1953) in the Palaus. Under favorable conditions, one generation, egg to egg, can be as short as 20 weeks. The total life span of individuals reaching maturity probably averages close to eight months, since there is evidence that grubs with prolonged development produce under-sized, short-lived adults.

TABLE 1. *Life cycle of the Coconut Rhinoceros Beetle,* Oryctes rhinoceros.

Stage	Activity	Duration
Egg	Incubation	11 days
Larva	Feeding and moulting	
L_1		3 weeks
L_2		3 weeks
L_3		5 to 9 weeks
Pupa	Pupation	3 weeks
Adult	Teneral in pupal chamber	3 weeks
	First feeding	1 week
	Dispersal, mating (and oviposition)	2 weeks
	Subsequent feeding and ground visits	12 weeks

OVIPOSITION.—Apparently almost any log or heap soft enough for burrowing, yet firm enough to provide compacted frass, may be utilized for oviposition. The female beetle makes a serpentine burrow, laying eggs one by one and compressing the chewed material behind her. At first soft and oblong, the egg swells into a rubbery globe four or five days after oviposition. *O. rhinoceros* eggs were most commonly found in coconut logs or stumps, but they were also collected under or in other logs (pandanus, sago, breadfruit, kapok, erythrine, etc.) and from heaps of sawdust, grass, or refuse. The largest number found in any one site was 87, removed from the fibrous tip of a young palm blown down by a hurricane six months earlier. Other collections indicated that ovipositions in such soft material near the crown-trunk junction may have occurred less than a month after the hurricane. Similar results were obtained with logs exposed in grassy areas both in Western Samoa and Malaysia. In the Samoan trial, the first oviposition apparently was made under the "bark" of a log 40 days after installation. Later oviposition burrows were more apt to be in the log ends, corroborating the sequence described by Cumber (1957) for coconut stumps. After one year of exposure in grassy areas, 12 of the 25 coconut logs in Malaysia and 45 of the 100 logs in Samoa had served, at least once, as oviposition sites. However, in Malaysia, 43 of the 50 logs in fern areas and, in Samoa, 29 of the 30 logs under dense cocoa canopy were still so hard that they could not readily be used for oviposition burrowing. The cocoa-shaded logs were first used as oviposition sites 15 months after installation.

The number of eggs laid during each oviposition was determined by using the coconut cap technique described earlier. In 42 trials, clutch size ranged from 11 to 62 and averaged 27. More eggs were laid by larger female beetles than by small ones. Those with a mean length of 36 mm averaged 22 eggs; 40 mm, 29 eggs; and 46 mm, 38 eggs. Since the average length of 631 female beetles in Samoa was 42.5 mm (the average for 762 male beetles was 41.1 mm), the normal clutch size should be close to 30. This estimate was supported by dissection of 145 gravid female beetles caught in artificial stump traps, or at light. Full-sized eggs averaged 22 in these beetles, and their ovaries contained others which presumably would mature during the oviposition period. The actual rate of oviposition reached 14 per day under optimal burrowing conditions but 4 or 5 per day was more typical. It is not known how many clutches are laid by each female beetle, but the cap experiments showed that they could lay a clutch every three weeks. If they live 15 weeks, they might be able to lay as many as 5 clutches, totaling 150 eggs. A conservative estimate, more in line with Gressitt's (1953) observations, would be 3 or 4 clutches, totaling between 90 and 120 eggs.

LARVAL DEVELOPMENT.—After eclosion, the first instar grubs consume the chorions and start feeding on the burrow frass. In soft logs or heaps, the grubs can disperse freely from the oviposition site. Under such favorable conditions, development proceeds rapidly, and the third instar may be attained in six weeks. The larger grubs appear to avoid one another and are spaced out within the site. Simple laboratory trials with heat gradients in a compost-filled tray showed that grubs also avoid zones heated above 37° C (100° F), which would limit their movement in sun-heated logs or fermenting heaps. An analysis of larval density in important categories of sites is presented in table 2. The minimum volumes per grub were 400 cc in a coconut log; 5000 cc in a kapok log; 7000 cc in a breadfruit log; 7000 cc in sawdust; and 9000 cc in grass compost. Some larvae were found in sites where they would have little chance of getting enough nourishment to complete their development. Examples would include very hard breadfruit logs and rotten papaya stems. In the latter situation larvae were, however, able to reach the third instar.

TABLE 2. *Density of* Oryctes rhinoceros *larvae in ground sites.*

	Coconut logs and stumps	Other logs	Organic heaps
Number of sites	90	26	18
Average volume cc	52,000	116,000	2,000,000*
Larvae	1167	220	795
Average volume per larva	4000	14,000	40,000*

* Approximate.

Larval mortality is quite important and will be discussed later.

PUPATION.—The late third instar larva in a partly decomposed log usually burrows into a firm portion of the log prior to pupation. Similarly, it may burrow down from a soft heap into the ground beneath. Only under certain circumstances, not yet clearly defined, does the grub form a pseudo-cocoon of compacted fiber or frass. When the pupal chamber has been formed, the larva goes through a non-feeding prepupal period lasting approximately one week (Gressitt 1953).

ADULT FEEDING, DISPERSAL, AND MATING.—After the teneral period, during which the exoskeleton darkens and hardens, the adult beetle chews out of the pupal chamber and flies to a palm. In most areas where palms were abundant, it was unusual for more than one beetle to feed in a palm at the same time. However, isolated palms and those along the inland margins of plantations sometimes were simultaneously attacked by several beetles. Even under such crowded conditions, each was more apt to make its own feeding burrow than to use one made by another beetle.

Each feeding visit generally caused either petiole or leaflet damage to three or four fronds (Hinckley 1966). Burrow depths in the crowns of 2- to 10-year-old palms were measured in three areas along plantation margins. For 116 burrows occupied by beetles, the average depth was 16 cm. Measurements in 63 burrows so recently vacated that they had not been distorted by the growth of the palm gave an average depth of 21 cm. The range, both for empty and occupied burrows, was from 2 cm to 50 cm. An empty 2 cm burrow presumably represented an abortive feeding effort, whereas a 50 cm burrow may have been made by two beetles feeding sequentially. Deep burrows on young palms were often lethal, either through direct injury to the growing tip or from secondary infections of bacteria and fungi. Coconut production is reduced by damage to unemerged spadices and by loss of photosynthetic surface on "cut" fronds.

To determine the rate of penetration and the length of stay, additional observations were made. In 30 trials, beetles were put into 4-cm-deep holes bored, with brace and bit, in young growing palms. In 15 of these trials, the beetles fed and their average stay was six days (range: 4 to 8 days). In the insectary, beetles bored into moist palm petioles or stalks of sugar cane. Duration of stay for 10 trials with petiole feeding averaged 7 days and for 20 trials with cane feeding, 6 days. A behavior pattern that would explain laboratory and field observations is penetration at a rate of 5 cm per day for 3 days, followed by 3 days of less active burrowing with an average penetration of 2 cm per day. Weight measurements also fitted this pattern. Typically, a beetle with the normal weight of 5.5 gm reached a peak of 7 gm 3 or 4 days after it started feeding and showed no gain thereafter. Two weeks after feeding, its weight would drop to 4 gm.

The normal interval between feedings is probably more than 10 but less than 20 days. Beetles unfed for more than 20 days may be too weak for a return flight to a palm and therefore die in a ground site. There is also evidence supporting the concept of a post-feeding dispersal period lasting up to a week. Beetles freshly fed on a palm were flown on a tether in the laboratory. Their flight duration averaged between 2 and 3 hours. Distances travelled were between 2 and 4 km. Beetles exhausted by such long flights were held in moist soil or wood for a day or two, after which they could again fly, although seldom longer than 30 minutes. The fact that even mated female beetles taken from palms rarely contained full-sized eggs also points to the existence of a post-feeding period of dispersal, egg maturation, and oviposition site selection. The male beetles apparently make more flights during the dispersal period since more are caught in the stump traps. The total catch during the period between October 1964 and December 1966 included 3049 male beetles and 1988 female beetles. This 1.5 to 1 ratio is known to be abnormal since larval sexing confirmed the 1 to 1 ratio recorded by Gressitt (1953). The male beetles were not affected by the presence or prior presence of female beetles, virgin or mated, in the traps.

In the laboratory, mating could take place prior to the first feeding. However, after being held for a month to 6 weeks in coconut caps or sawdust, only 3 out of 15 mated and only one of these developed a full clutch of eggs (21). Unfed beetles showed signs of egg development, and when fed but not mated female beetles sometimes laid a few inviable eggs.

Virgin female beetles were often collected from palms, and it seems probable that mating does not occur until the beetles have flown away from the palm crowns. Male beetles readily burrow into logs (Cumber 1957), and pairs in copula, with the male at a right angle to the female, were found under logs. Although the great distension of the bursa copulatrix in many of the female beetles indicated that multiple matings were common, a female beetle could continue to lay viable eggs for several months after one mating.

MORTALITY PATTERNS.—By following the fate of natural or artificial cohorts, it was possible to estimate larval survival to pupation (table 3). The

TABLE 3. *Survival of* Oryctes rhinoceros *larvae.*

	Initial number of larvae	Estimated survival to pupation
		(%)
Coconut logs stocked with:		
Female beetles	450[1]	5
Eggs	180	1
Larvae	430	1
Heaps stocked with:		
Female beetles	50	2
Larvae	258	1
Coconut logs naturally infested	1300*	1.2

* Approximate.

highest survival was observed in soft coconut logs which had been stocked with female beetles. Monthly inspections lowered survival, and the densest larval populations were obtained in logs left undisturbed for 4 months after oviposition. About 20 percent of the grubs reached the third instar (L_3) in the disturbed logs, and 50 percent in the undisturbed logs. Even in the undisturbed logs, few grubs were able to reach the prepupal state.

It appears likely that larval mortality has two peaks, initially when the first instar (L_1) leaves the oviposition frass and tries to feed on harder wood and later when the L_3 is unable to accumulate enough fat reserve for pupation. The high incidence of prolonged third instars and under-sized adults symptomizes the second hazardous period.

Mortality caused by predators, parasitoids, and pathogens was less common than that attributable to malnutrition. The only eggs removed by ants or killed by desiccation were those exposed artificially. When laid by a female beetle in an oviposition burrow, the eggs were protected from most hazards. Similarly, aside from the rare *Metarrhizium* fungal infection, the pupa suffered no mortality in its chamber. About 10-20 percent of the larvae were infected by *Metarrhizium*, a level which may have increased through synergism with a virus recently introduced from Malaya (Marschall 1970). Some grubs in coconut logs were eaten by rodents, and some in sawdust heaps were consumed by larvae of the elaterid beetle, *Lanelater fuscipes* (F), or parasitized by the scoliid wasp, *Scolia ruficornis* F. The centipede, *Scolopendra morsitans* L., was present both under logs and in sawdust heaps, and may have killed some accessible grubs. Generally, *Oryctes rhinoceros* immature stages within a coconut log are well protected from any natural enemy now present in Samoa (Hinckley 1967). In his survey of the Asian tropics, Paine (1967) examined "nearly 300 dead coconuts and 80 trunks of other palms" but found little evidence of effective parasitization or predation.

DISCUSSION

As noted by Dry (1922), larval mortality is high for species of *Oryctes* and for many other xylophagous insects. He implied, and I would agree, that this mortality is caused more by various forms of malnutrition than by cannibalism, predation, or infectious diseases. The deficiencies leading to malnutrition and death have yet to be determined, but hardness, high lignin content, or fungal permeation of logs may be involved. Under these conditions, it is quite possible that natural enemies and pathogens have little effect on the dynamics of *O. rhinoceros* populations. Most of the grubs killed by such agents would have died anyway before reaching the pupal stage. Thus, the entomophagous organisms should not be expected to have an important role in controlling Rhinoceros Beetle outbreaks.

In this connection, it is helpful to examine the phrase "breeding site." For *O. rhinoceros,* a coconut log can be the site of mating, oviposition, larval feeding, pupation, and adult emergence. However, the site contributes to the perpetuation of the population only when the last stage, adult emergence, is achieved. Less optimal sites, such as a hard new log, an old rotten one, or a heap saturated with *Metarrhizium* spores, may even serve as lethal traps since the probability of egg to adult survival is low. The same reasoning applies to any of the outbreak situations described in the introduction. It can also be applied in analyzing the population dynamics of bark beetles, mosquitoes, or any organisms with specialized breeding sites. The quality, distribution, and abundance of their breeding locations may determine adult numbers.

Small improvements in the average survival of larvae would explain the post-typhoon increases in Rhinoceros Beetle populations so often observed on Pacific islands. Assuming survival from oviposition to adult emergence is near 2 percent in a stable population,[2] a posttyphoon generation might increase 2½ times with an average 5 percent survival in the numerous palm logs felled by the storm. A population decline would be expected only when preadult mortality exceeds 98 percent.

The identification, and destruction or removal, of productive breeding sites is an essential prerequisite to success in any campaign against the Rhinoceros Beetle. The strategy of control should include priorities based on understanding of Rhinoceros Beetle ecology and behavior. Well-shaded or hidden logs can be left while more exposed stumps and logs are destroyed. Sites known to be accessible but lethal can also be maintained. The final goal should be a population reduction below the level at which economic damage[3] can be detected (Hinckley 1966).

[2] With a 1 to 1 sex ratio and each female beetle laying 90 to 120 eggs, this would yield approximate female replacement.

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[3] About 7.5 beetles/hectare (3/acre) on plantations in Western Samoa.

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