BIOLOGY, ECOLOGY, AND CONTROL OF PALM RHINOCEROS BEETLES

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INTRODUCTION AND HISTORICAL OVERVIEW

Palms are important crops in the tropics. The coconut palm (*Cocos nucifera*) produces nuts which may be used directly for food, or the contained copra may be crushed to yield coconut oil. The oil palm (*Elais guineensis*) produces bunches of fruits that yield both palm oil and kernel oil, and the product of the date palm (*Phoenix dactylifera*) is well known. The Rhinoceros beetles (Scarabaeidae, Dynastinae) are important pests of palms. Attacks by adults may reduce yield, kill both seedlings and young and old palms, and discourage replanting. They may provide entry points for lethal secondary attacks by the palm weevil *Rhynchophorus* in some countries or by pathogens. The breeding sites in which the immature stages develop are widespread, abundant, and often difficult to remove or destroy. The main pest species are members of the genus *Oryctes*, particularly *O. rhinoceros* [which caused damage estimated as at least $US 1,100,000 to South Pacific countries in 1968 alone (20)], *O. monoceros*, and *O. boas;* subspecies of *Scapanes australis;* and species of *Strategus*.

Much of the earlier work was reviewed by Gressitt (56), and this review emphasizes developments since then, although reference is made to the earlier studies where appropriate. Integrated pest control (in the sense of using several compatible control methods simultaneously in an effort to reduce pest numbers to a subeconomic level) was attempted for decades. However, results were frequently unsatisfactory or disappointing, and control was often affected by the economics of, and local attitudes towards, the

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crop. The vigor of application of the methods often fluctuated with the changing market value of the crop, and it was difficult to have the control measures carried out uniformly by all sectors of the communities concerned. Only in recent years has the development of new measures, such as the use of baculovirus and cover crops, added highly effective and practicable components to integrated control programs.

TAXONOMIC STUDIES

Thirty-nine species of *Oryctes* were recognized in a recent comprehensive study (37, 38). Of these, 11 species are endemic in Madagascar and 5 in the Comores (139), 3 in Mauritius (176), and several in Africa (44, 45). Four subspecies of *Scapanes australis* have been recognized (35, 39). Two comprehensive revisions of *Strategus* have recently appeared: Endrödi (40) recognized 25 species and illustrated male genitalia; Ratcliffe (152) recognized 31 extant species and gave distribution maps, photographs, and male genitalia illustrations for all species. The taxonomy of the following minor pests has recently been revised: *Xylotrupes gideon* (16 subspecies) (41), *Chalcosoma,* spp. including *C. atlas* (41), *Trichogomphus* (9 species) (39), and *Papuana* spp. (36). The larvae are far less well known and only the following have been described according to Ritcher's method (154): *O. boas* (129), *O. gigas* (130), *O. monoceros* (16), *O. rhinoceros,* three subspecies of *S. australis, Trichogomphus fairmairei* (= *T. excavatus*), *X. gideon* (6), and *C. atlas* (12).

DISTRIBUTION AND SPREAD TO NEW AREAS

O. rhinoceros is endemic to the coconut growing regions of Asia (20) from west Pakistan, through India, the Maldive Islands, Ceylon, Hainan, Taiwan, Hongkong, Thailand, Vietnam (171), the Malayan Peninsula, the islands of Java, Sumatra, Bali, Lombok, Kalimantan, Celebes, Ceram, and Amboina in Indonesia (191), to the Philippine Islands. In Burma the pest first appeared in the extreme south of the peninsula. It probably entered from Malaysia about 1895 and worked its way north throughout the coconut growing areas of lower Burma over the following 15 years (114). It was accidentally introduced to a number of copra-producing areas of the Pacific and Indian oceans. It is believed to have been introduced in rubber seedling potplants from Ceylon to the Pacific island of Upolu, Western Samoa in 1909 (86); from there it spread to the neighboring island of Savai'i and to Tutuila in American Samoa. In 1921 the beetle was recorded in Niuatoputapu (Keppel) Island in the Kingdom of Tonga, but it was successfully eradicated in a campaign from 1922 to 1930. Wallis Island, about 320

km west of Samoa, became infested in 1931 (22). During the Second World War there was an increase in aircraft and shipping activity in the Pacific region; the beetle was introduced to the Palau Islands about 1942 (56), New Britain in 1942, and West Irian (20). Further establishments occurred in Vavau (Tonga), 1952 (34); New Ireland, 1952; Pak Island and Manus Island (New Guinea), 1960; Tongatapu (Tonga), 1961; and the Tokelau Islands, 1963. The beetle was found at Suva on Viti Levu (main island of the Fiji group) early in 1953 (167), and it has now spread to at least 42 islands of the group, including all the important copra-producing ones, despite an intensive quarantine program to prevent this (11). In the Indian Ocean the island of Diego Garcia was infested during the First World War, possibly by beetles carried on troopships (135). Specimens were collected in the Cocos (Keeling) Islands in 1940. In July 1962 it was found in Mauritius (177) and in 1978 in Reunion (121).

    O. monoceros and *O. boas* are endemic in east and west Africa; the former also occurs in the Seychelles Islands (174). *Oryctes* spp. that attack date palms are distributed as follows: *O. sahariensis* in Chad and Sudan; *O. agamemnon* (= *O. sinaicus*) in the Sinai Peninsula, Saudi Arabia, and the Persian Gulf coast of Iran; and *O. elegans* in the Mesopotamian region of Iraq and in neighboring Iran (29). The four subspecies of *S. australis* are distributed as follows: *S. a. australis* on the Papua New Guinea mainland west of the Huon Gulf, *S. a. brevicornis* east of the Gulf, *S. a. grossepunctatus* in New Britain and New Ireland, and *S. a. salomonensis* on Bougainville and a number of the Solomon Islands (13, 35, 39). The distribution of the geographical subspecies of *X. gideon* has been mapped (41) and extends from the Himalayas, India and Sri Lanka eastwards throughout southeast Asia to Papua New Guinea, north Queensland, and the New Hebrides.

BREEDING SITES

Large numbers of *O. rhinoceros* larvae may develop in the tops of dead standing coconut palms that have been killed by adult beetle attacks or lightning strike (13, 27, 96, 166), war damage [e.g. Palau Islands (56), Philippines (162)], or other causes. In the Philippines, palms killed by cadang-cadang disease become breeding sites (162). Coconut stumps and logs on the ground are also important breeding sites (56, 135). Floating logs containing larvae in tunnels might spread the pest to new areas (96). The insect may also breed in other types of decaying wood, compost, and sawdust heaps in Tonga, Samoa, and Fiji; decaying *Pandanus* trunks in the Palaus (56); and heaps of decaying cocoa pod shells in New Ireland (13). In India (93, 127) and Mauritius (121) heaps of cattle dung were the most important sites, whereas in Burma dead coconut stems, heaps of rotting

paddy straw, and farmyard manure were most important (53). In Malaysia larvae developed in decaying rubber stumps (2). It was reported that larvae occurred in rubbish in the axils of living palms when ground breeding sites were unavailable (124). Mackie (99) stated that in the Philippines breeding could occur in piles of rotting coconut husks, but other authors have not confirmed this. Dead standing coconut trunks and fallen logs are used by a number of *Oryctes* spp. in Madagascar (3). *O. monoceros* breeds in dead standing conconut and oil palms in Sierra Leone (63), Nigeria (65), and the Ivory Coast (103), and in decaying coconut logs in Zanzibar (101), Kenya (33), and Seychelles (174). *O. owariensis* breeds in dead standing oil palm, coconut, and *Raphia* trunks in Sierra Leone (63, 65); *O. ohausi* in standing rotten *Raphia* palm trunks in Nigeria (65); and *O. sjöstedti* in debris in dead leaf bases just below crowns of oil palms in Nigeria (65). In Togo the numerous palms killed by Kaincopé disease become *Oryctes* breeding sites (103), and the same applies to old oil palms poisoned with diquat in Nigeria (156). *O. centaurus* in Papau New Guinea breeds mainly in dead standing sago palm trunks (*Metroxylon sagu*) but may also use dead coconut poles (14, 66). *O. boas* breeds in manure heaps (63, 65, 101) but not in rotting wood. In Iraq, *O. elegans* breeds in the stems of dying or newly dead date palms (85); in Iran it breeds in dead trunks or in litter in the axils of fronds (52).

There has been considerable confusion in the literature concerning the breeding sites of *S. australis;* many earlier authors assumed that they were identical to those of *O. rhinoceros* (97, 134, 138, 146, 163). However this assumption has been shown to be invalid, and it is now established that *Scapanes* breeds under the decaying trunks and stumps of bush trees and occasionally in rotting moist humus beneath heaps of decaying cocoa pod shells (13, 14). *X. gideon* breeds in rotten leaves, decayed wood, compost, and at the surface of the soil beneath decaying coconut logs (7). *T. fair-mairei* breeds in tunnels in root masses of ferns, belonging to the *Asplenium nidus* group, that grow on branches of living trees (6). In Puerto Rico, *Strategus quadrifoveatus* (= *S. oblongus*) breeds in decaying coconut logs and other wood (142).

BIOLOGY OF THE IMMATURE STAGES

The duration of the immature stages of *O. rhinoceros* has been studied by various authors under differing conditions (13, 20, 21, 51, 54, 56, 62, 80, 93, 124). General figures based on four publications (13, 20, 62, 80) are shown in Table 1, as well as laboratory results for *O. boas* (75), *O. elegans* (81), *O. monoceros* (82), *Scapanes australis grossepunctatus* (13), and *Strategus aloeus* (84). Some figures are available for *S. quadrifoveatus* (142).

The immature stages of *Scapanes* last much longer than those of the *Oryctes* species.

Unfavorable climatic or nutritional conditions for *O. rhinoceros* delayed larval development, which was extended to as long as 14 months, and smaller than average adults were sometimes produced (20). When the larvae of *O. elegans, O. rhinoceros,* and *O. monoceros* were fed living vegetable material in the laboratory, those of *O. elegans* developed best (which is perhaps correlated with the ability of these larvae to damage date palms), whereas those of *O. monoceros* developed most poorly. However, for all three species development was slower and the resulting adults smaller and less fecund than when the larvae were fed on dead plant material (76). In a study of their sensory physiology, *O. rhinoceros* larvae were allowed a choice between different conditions in a circular area (21 cm in diameter) divided into two halves (25). The larvae preferred a temperature of 27–29°C and avoided higher or lower temperatures. They were attracted by the smell of ammonia and acetone (perhaps present in natural breeding sites) and repelled by acetic acid. Movement was momentarily arrested by sudden exposure to bright light, and the larvae then moved to the shaded area. Larval behavior was dominated by the light factor. In the natural environment, if larvae are placed on the surface of breeding medium, they quickly burrow down out of sight; this strong negative phototaxis is probably an adaptation against desiccation and predation. Lower humidities were avoided and higher relative humidities (85–95%) always selected. These mechanisms singly or in combination keep the larvae out of areas that are unfavorable for survival or development.

The late third instar larva in a partly decomposed log usually burrows into a firm part of the log prior to pupation. If it is in a soft heap it may

Table 1   Duration in days of immature stages of some palm rhinoceros beetles

Stage	Oryctes rhinoceros	Oryctes boas	Oryctes monoceros	Oryctes elegans	Scapanes australis	Strategus aloeus
	(13, 20, 62, 80)	(75)	(82)	(81) mean	(13)	(84)
Egg	8–12	7	14	10	32	21
First instar larva	10–21	10	13	14	35	14
Second instar larva	12–21	14	12	21	45	21
Third instar larva	60–165	70	56	56	190	210
Prepupa	8–13	8	9	10	21	14
Pupa	17–28	15	17	14	45	42

burrow down into the soil beneath. When reared in friable material, a roomy cocoon with a smooth inner surface is formed from compacted medium (10, 13). In this cocoon a nonfeeding prepupal period is followed by the pupal and teneral adult phases.

FEEDING AND DAMAGE CAUSED BY ADULTS

Host Plants

Gressitt (56) gave a comprehensive list of food plants used by *O. rhinoceros* in addition to coconut and oil palms. Lists of host plants have been noted for India (115, 127), Indonesia (91), and the Philippines (99). In Mauritius, ornamentals such as the royal palm (*Roystonea regia*), the latanier palm (*Livistona chinensis*), the talipot palm (*Corypha umbraculifera*), and the raphia palm (*Raphia ruffia*) are attacked (121). *S. quadrifoveatus* feeds on several species of palm and occasionally on sugarcane stalks (142). Besides palms, *Scapanes australis* subspecies bore into the stems of banana plants (*Musa sapientum*) and Manila hemp (*Musa textilis*) (13, 169).

Mode of Attack and Effect of Damage

The way in which *O. rhinoceros* attacks coconut palms, and the resulting V or wedge-shaped appearance of the cut fronds have been described and illustrated by several authors (e.g. 27, 51, 62, 86, 99, 124). Attacks tend to be concentrated on the margins of palm groves and on taller, more prominent palms (27, 183). One attack increases the likelihood of further attacks (8, 183), i.e. certain palms are more frequently attacked than would be expected by chance. More than one beetle may attack a palm at the same time, while a neighboring palm may be unattacked (56). In badly infested areas in India, five to six beetles have been found feeding in the same crown (124).

The structure of the crown in relation to beetle attacks has been comprehensively described (183). The central cluster consists of four to eight spears (very young fronds, which have not yet unfurled to expose and extend their leaflets). After unfurling, the midrib or rachis of the frond makes an angle with the stem (the axil). The axil of the youngest (i.e. uppermost) unfurling frond is (designated) axil 1, and lower, older fronds are numbered sequentially. In each axil a spadix bearing both male and female flowers develops into an inflorescence, which is at first enclosed by a spathe of sheathing bracts.

Studies in Western Samoa (183) showed that most attacks begin in axils of opened fronds 4–6; very few attacks begin below frond 8. The lower the attack site, the more fronds will be damaged and the closer the beetle will come to the inflorescences and the central growing points. Such lower

attacks are dangerous, but rare. Attacking higher axils is advantageous to the beetle because the tissues are softer. The burrow has a short, straight horizontal section leading into the palm center, from which a longer vertical tunnel penetrates 15–50 cm down into the center of the spear cluster. The beetle feeds on tissue juices. Some of the crushed fibre is pushed outside the entrance hole, where it indicates the insect's presence (99). For 116 occupied burrows measured in crowns of 2- to 10-year-old palms, the average depth was 16 cm; 63 recently vacated burrows showed an average depth of 21 cm; the range for both empty and occupied burrows was 2–50 cm (62). An experiment in which beetles were placed in artificial holes 4 cm deep indicated an average stay of 6 days (range 4–8 days) and a penetration rate of 5 cm/day for 3 days, followed by 3 days of less active burrowing (2 cm/day) (62). Results in Indonesia indicated a stay of 5–10 days (91). In New Britain a male/female sex ratio of 0.91 for beetles in crowns occurred (8). Most females had immature oocytes in the ovaries.

There is no exit burrow, and if a beetle remains up to about 9 days in its feeding burrow, palm growth will carry the entrance upwards and clear of the stipule (the coarse fibrous band enclosing the frond base), allowing the insect to escape easily (183). The central vertical feeding burrow may appear to be harmful to the palm but in fact often causes little real damage. If the burrow goes deep enough it may cut across the top of a very young spear, and if very deep it may destroy the growing point, but probably few palms are directly killed in this manner. The short horizontal entrance burrow, cutting directly across petioles (lower part of midribs) and spears (truncating fronds and leaflets) causes far greater damage. Older palms have a more compact crown and therefore have more fronds affected by a single attack than younger palms. An attack damaged an average of 4.2 fronds; 3.6 fronds had damaged leaflets on 9-year-old palms, and 4.3 to 5.9 fronds were damaged on older palms. Earlier estimates were 2–3 fronds damaged by an attack (60), or up to 5 fronds (27). Each attack on 9-year-old palms cut out approximately 0.41 of a frond, except where part or the whole frond broke off in windy areas because of a damaged midrib or petiole (183). The time span from the initial penetration by the beetle until the damage first became visible from the ground averaged 41 days, and it was 113 days before all damage became visible. Except where inflorescences were directly damaged, no immediate effect of the attacks on flowering and nut bearing could be determined. The long-term effect of weakening due to leaf reduction could not be quantified because attacks occurred very irregularly and the study did not continue long enough. Sison (162) stated that palms with 50% of all their fronds damaged had about one-fifth the number of developing nuts that are found on normal palms. Many immature nuts were dropped by the damaged palms.

Pruning experiments were therefore conducted (183). In one trial, 12 fronds were cut from palms over a period of 20 months—equivalent to the effect of 30 separate attacks at a rate of 1.5/month; in another trial, pruning equivalent to 15 attacks in 20 months was performed. The palms responded to frond loss by increasing the drop-off of immature button nuts during the early shedding phase and by aborting entire inflorescences a few months before natural flowering time. Pruning equivalent to 1.5 attacks/month would have killed the palms if sustained long enough, even though the growing points were undamaged. However this pruning was more severe than the normal level of beetle damage. The rate of frond replacement, number of flowers on each inflorescence, and rate of growth of nuts held to maturity were scarcely, if at all, affected. The results of the pruning study showed how yield is affected, but did not show the size of the effect. Experiments in India showed that large scale cutting of younger fronds may cause considerable reduction in yield of nuts as long as the practice is continued (102). Many difficulties are encountered in studying the effect of beetle attack on yield (149, 150, 183), and a full analysis of the problem remains to be carried out.

On oil palms *O. rhinoceros* bores into the base of the cluster of spears, causing wedge-shaped cuts in the unfolded fronds. In young palms where the spears are narrower and penetration may occur lower down, the effects of damage can be much more severe than in older palms (179, 181). Pathogens may enter the wound and cause secondary rotting of the bud. Sometimes the new spears of a palm recovering from attack may grow through the hole made by the beetle when it entered the spear cluster. Palms less than a year old are often killed by the attack, but the likelihood that the damage will prove lethal declines rapidly as the palms mature.

Damage by *O. monoceros* to coconuts has been studied in the Ivory Coast (103, 106, 108, 109). In palms aged 1–2 years, 36% of attacks occurred in the axil of the third unfurled frond from the top. In palms three or more years old, 50% of attacks occurred in the axil of the second frond from the top. One attack damaged 75% of the young fronds in the spear cluster, i.e. 2–4 fronds. The number of fronds affected depended on the length of the burrow, which was as much as 1 m but usually averaged 45 cm in adult palms (106, 109). On young palms the beetle only needed to burrow a short distance in order to reach the growing point and kill or severely deform the palm. However, attacks on older palms were rarely lethal. The insect burrowed 4.2 cm/day, and stayed about 9 days in its tunnel. The central spear cluster grows about 4 cm/day and counterbalances boring of the beetle in the wet season, but growth is much slower in the dry season. In a plantation of 4-year-old palms, 70% of attacks occurred in the first six rows, with 50% in the first three rows, whereas in a planting of 2-year-old palms, the first

12 rows received 70% of the attacks. Taller palms received more attacks than younger lower palms (silhouette effect). Even in young plantations certain palms were attacked repeatedly while similar-sized neighbours were not infested. Possibly beetles are attracted by odors from the damaged tissue (106). On some plantations of 2½–3-year-old coconut palms in Zanzibar, *O. monoceros* killed more than half and retarded the growth of others. Mature palms were also attacked, but the damage was not serious. Isolated palms and those on poor soil were more often attacked than those in dense groves (101). In Kenya it was also observed that attacks occurred more frequently to palms in outer plantation rows (33). At one locality deaths of bearing palms average 2% per year. Assuming replanting took place immediately, this represents about a 15% loss of bearing capacity, because the replants require 7–8 years to come into bearing (178). In the Seychelles seedling coconuts were killed or the palms were seriously damaged during their first 5–7 years of life (113, 174).

In Madagascar *O. simiar* attacks coconut palms coming into bearing in a manner similar to that of *O. rhinoceros*. It also bores into the leaf bases of banana plants (3). *O. pyrrhus* burrows into the soil to attack coconut seedlings at the junction of stem and nut (3, 166) and at the bases of 4-year-old oil palms. *O. ranavalo* tunnels into moist soil to attack the bases of bamboo plants (3).

Scapanes australis usually restricts its attacks to young coconuts, from just past the seedling stage to about five years of age (13, 14, 164, 165). The beetles crawl down an axil before boring into the heart of the stem, or they bore straight into the trunk from the outside. Because it readily attacks very young palms which cannot sustain much damage and consequently are often killed, it is a more serious pest in Melanesia than *O. rhinoceros*. More males than females were removed from holes in New Britain. The male/female sex ratio was about 3.6, possibly because males spend more time visiting palms and feeding while females are presumably searching for breeding sites. Often more than one beetle occurred in the same hole; females were usually deeper inside than males (8). Sometimes the growing point of 1–2-year-old palms was not completely destroyed; however, the plant was always more or less deformed and produced twisted fronds with the leaflets compressed and crumpled together. Palms a little older when damaged often had the inner fronds invaded by termites and mealybugs. The incidence of *S. australis* attack varied greatly from one locality to another, but was highest in new plantings established near virgin forest. On young oil palms damage took the form of holes in the frond bases, midribs of fronds chewed through, ends of fronds V-cut, and stunting and twisting sideways of the growing point, with the leaflets of emerging fronds compressed and deformed. In a few cases the young oil palm was killed (13).

Strategus quadrifoveatus tunnels 4–6 cm into the soil and then attacks the base of the coconut seedling sprout or the stems of palms up to 3 years old, causing death of the plant. Liability to lethal attack declines rapidly after the young palm begins to form a trunk. Beetles may interrupt a feeding period in order to return to their burrows and make trips to the surface of the soil (142). When *Strategus aloeus* burrows into the soil, it starts 50 cm away from the palm; once it is under the stem base it tunnels up into the base, frequently reaching the growing point. Only plants 1–2 years old are attacked, mainly at the beginning of the rainy season (109). In west New Britain, *Papuana woodlarkiana* attacked the roots of young oil palm seedlings (wrapped in nursery bags) about 4 cm below the level of soil, causing severe root damage and death of seedlings. Subsequently the beetles moved downwards, pierced the bottoms of the bags, and entered the soil beneath to a depth of about 30 cm. Although the number of seedlings attacked at any one time is small, the number attacked during the several months that the seedlings are in the nursery is quite significant (30). *Xylotrupes gideon* feeds on newly opened coconut inflorescences (7) and is said to feed on the undersurface of frond midribs, causing the distal portion to break and hang down.

Methods of Damage Assessment

Two methods of damage assessment have been evolved in order to judge the effectiveness of control measures. In the detailed type of survey, random samples of 20–30 palms at various sites are numbered with paint. Periodically the number of fronds above the horizontal level in the crown of each palm is counted with the aid of binoculars, as well as the number of fronds which show beetle cuts (11, 182). Results are expressed as the percentage of fronds damaged at one site or at a group of sites combined. The method is time-consuming, as each palm should be examined from several sides. In the rapid survey method only the central 3–5 fronds of the crown, i.e. the most recently opened ones, are considered. Palms are scored as either damaged in these fronds or undamaged; the total number of fronds damaged is ignored. At a given locality, four observation points are selected. An observer goes to each point in turn, faces in a given direction, observes 25 palms clearly visible to him, and records the number showing central crown damage. The results of the four observations are summed to give the percentage of palms damaged for the area. To increase reliability, two or three observers can work together and the average of their results can be obtained. Provided that all observers use the same observation points and face the same direction, they need not observe the same individual palms (49).

An attempt has been made to correlate the following data: artificial reduction in leaf area, with reduction in nut production (49); the percentage

of fronds beetle-damaged on a sample of 100 palms, with an estimate of the percentage reduction in total leaf area; the percentage of fronds beetle-damaged in a sample of 500 palms, with the number of developing nuts; the percentage of beetle-damaged fronds, with the percentage of trees with central crown damage; and the percentage of centrally damaged trees and the percentage of fronds damaged, with estimated percentage nut loss.

Correlations between percentages of palms with central crown damage and percentages of nut loss yielded the following figures: 0–10% damaged, 1% loss; 10–20%, 4%; 20–30%, 6%; 30–40%, 8%; 40–60%, 12%; 60–80%, 17%; 80–100%, 23%. However it is not known how reliable these results were. Significant observational error may have occurred in estimating the percentage reduction in leaf area due to beetle cutting. There is a large standard error in correlating percentage of fronds that were beetle-cut with percentage of trees that had central damage. Also, the correlation between percentage of beetle-damaged fronds/tree and the number of developing nuts/tree was based on a sample at only one location. Palms at other locations, of different ages, growing on different soils, and under different climatic conditions may have their nut production affected to different degrees by beetle attack.

GENERAL BIOLOGY OF THE ADULTS

O. rhinoceros adults leave their pupation sites 20–30 days after ecdysis (188) and visit palms for feeding. Mating occurs in the breeding sites (27, 188). Multiple matings may occur (77) but are not essential, since spermatozoa retain their vitality for up to six months in the female's spermatheca (83). Laboratory studies have shown that 3-week-old females and 5-week-old males can mate before the first flight and feeding, i.e. oviposition can occur before beetles emerge from the breeding sites in which they developed (74, 188). However in the field, mating and oviposition usually take place after the young beetles have left the pupation site and after the first feeding (188). Under mass-rearing conditions at La Minière, France, the mean longevity was five months, but males died several weeks before females. The mean fecundity was 49 (80) or 60 eggs/female (83). In a New Britain insectary, adult males lived 6.4 months and females, 9.1 months, with a mean fecundity of 51 eggs (13), whereas in India the average longevity was 4.7 months (124). Information on tunnels in oviposition sites and on egg clutch size has been gathered in Western Samoa (62).

O. monoceros pairs were found in copula in decaying logs (33). Under mass-rearing conditions the mean longevity was three months, and fecundity was 25 eggs/female, with wide individual differences. Spermatozoa stored in the female's spermatheca remained viable for three months (83).

Field-collected adults lived more than 100 days after collection (33). The mean fecundity of *O. boas* was 40 eggs/female; oviposition commenced four weeks after the last molt and lasted 2–6 weeks during a longevity of 6–12 weeks, which allowed two generations per year (75). *O. elegans* began oviposition 2–3 weeks after pairing and the adults lived an average of four months, with a mean fecundity of 60 eggs/female (81). *Scapanes australis grossepunctatus* had a mean fecundity of 30 eggs/female and the mean adult life of both sexes was 115 days (13), whereas *X. gideon ulysses* males lived an average of 90 days and females, 102 days, with a mean fecundity of 55 eggs (7).

Apart from *X. gideon* and *Papuana* spp., rhinoceros beetles are rarely attracted to ordinary lights (142, 179). In laboratory studies *O. rhinoceros* crawled towards red and purple lights, in preference to other colors (55). It flew in the field mainly between 6 and 7 P.M. (96). Checks on young palms showed that 80% of *O. monoceros* and *O. boas* had made their flight by the third hour after nightfall (106). *O. rhinoceros* freshly fed on palm were flown on a tether in the laboratory; their flight lasted between 2–3 hr, and distances traveled were 2–4 km (62). Three beetles flew 680 m from the nearest land to a ship between 8 and 9 P.M. (131). In India many beetles dispersed only 180 m from their breeding sites (124). In 1883 all plant and animal life was destroyed on Krakatoa, Indonesia by the volcanic eruption. In 1919 damage was found on palms there, and also a dead beetle. The island is 19 km from the nearest neighbor, Sibesi, and 40 km from the nearest coast of Java and Sumatra. Beetles may have flown in or may have been carried as larvae in floating logs (96). Most *O. monoceros* adults that were tagged with iridium-192 and released from a central point in a plantation travelled a radius of 150–200 m to palm crowns (107).

MASS REARING

Mass rearing was pioneered by Hurpin and colleagues at La Minière, France for *O. elegans* (81), *O. monoceros* and *O. boas* (75, 82, 83), *O. rhinoceros* (80, 82, 83), and *Strategus aloeus* (84). A mixture of ⅔ parts decaying wood and ⅓ parts cowdung was prepared and allowed to stand while the heat of fermentation destroyed the spores of the pathogenic fungus *Metarrhizium anisopliae,* which had greatly hindered mass rearing previously (123). Larvae were held in this food medium singly or were bulked together in large containers at 28–30°C, and they eventually pupated in it, yielding 60–80 adults for every 100 larvae. *O. monoceros* adults emerged about 14 weeks after the eggs hatched, and *O. rhinoceros* adults after 30 weeks (82). Adults were confined as single couples, or several couples together, in containers that were one-third filled with leaf mold or rotted sawdust in which they mated and oviposited; they were fed on

banana slices placed on the surface of the medium twice weekly. A 50 liter tank that enclosed 8–10 couples has proved very convenient and needs less handling (83). Longevity and fecundity under these conditions have been mentioned in the previous section. Bedford (10) used a similar method for *O. rhinoceros* in Fiji but preferred to steam-sterilize the larval food and oviposition media because of the widespread occurrence of *Metarrhizium* and baculovirus in sawdust heaps. Also, the eggs and young larvae were kept bulked but were separated into individual tins at the early third instar so that, should any case of fungus or virus occur, it would be confined to particular tins and would not affect all the larvae or pupae in an entire bulk box. Rearing was done at ambient temperature. The fecundity was 40 eggs/female; fertility of eggs was 53%; yield of third instar larvae from eggs, 42%; yield of adults reared from eggs, 38%; and total duration from egg hatching to emergence of adults from cocoons was 274 days. Wages were the biggest cost component. In 1974–1975 the cost of producing a beetle was $F 0.74, far cheaper than the cost of field collection.

In mass rearing in Western Samoa (155) the rate of growth of *O. rhinoceros* larvae was faster on a mixture of unfermented kapok wood and cowdung than on a mixture fermented for several days at 70°C. Perhaps the fermentation reduces the nutritive value of the mixture. Onset of pupation could be induced by transferring larvae 21–27 weeks old from 28°C to 25°C. Pupation then occurred at least one month earlier than when the larvae were left in the warmer temperature. In a container 95% of the larvae became prepupae within a week of each other. Where young and old larvae were present in a container, the young larvae at first prevented the pupation of the older ones. Later, however, the pupation of younger larvae was faster in the presence of older larvae. A similar phenomenon is found in field breeding sites where the pupation of a group of larvae apparently is synchronized. A strain of females was selected that gave higher egg production (3.52 eggs/female/week) than normal (2.72 eggs/female/week) and lived four weeks longer than the normal strain.

S. a. grossepunctatus were fed on sugar cane and would oviposit only in boxes of black soil (13). Only 18% of the eggs hatched. Larvae developed well in individual tins of a cowdung/sawdust mixture, which they eventually compacted to form the pupal chamber. *X. gideon* oviposited in boxes of rotted sawdust and the larvae were reared in the same manner as *Scapanes* (7).

NATURAL ENEMIES AND BIOLOGICAL CONTROL

Arthropod Parasites and Predators

In earlier years much effort was devoted to widespread searches for parasites and predators of *Oryctes* spp. in the hope of introducing them to new

areas for the control of *O. rhinoceros* (68, 73). However results have been disappointing, because few significant enemies were found or they failed to become established when transferred to new areas; and if they became established they failed to exert significant control over *O. rhinoceros* populations. The wasp *Scolia oryctophaga* was introduced from Madagascar to Mauritius in 1917 against the sugar cane pest *O. tarandus* (28) and apparently reduced its numbers, but the extent of this control has never been determined (122) and it did not prevent *O. rhinoceros* from becoming a pest there. *S. oryctophaga* did not become established in the Pacific (157). *Scolia ruficornis* was sent from Zanzibar to Western Samoa in 1945 and was recovered in 1949 (158, 160, 161), but it did not reduce the *O. rhinoceros* population to a subeconomic level (61). It was established in the Palau Islands by 1953 (136), and it was sent to Diego Garcia in 1951 and recovered in 1956 but was not effective in controlling *O. rhinoceros* there (135). It was released in the Gazelle Peninsula of New Britain in the early 1950s but was not found during 1968–1971 (13). *Scolia procer* parasitizes *O. rhinoceros* and *Chalcosoma atlas* larvae in logs in Malaysia (67, 179) and was released in Tonga in 1974 (49).

The carabid beetle *Neochryopus savagei,* which is predaceous both as larvae and adults on *Oryctes* larvae in Nigeria (65), was shipped to Fiji (133) and New Guinea, but whether it became established is doubtful. The carabid *Pherosophus* sp. was introduced from India (151) to Mauritius and became established there, but it did not significantly control *O. rhinoceros* larvae (121). Two species of elaterids with larvae predaceous on *O. rhinoceros* larvae are established in Western Samoa, but their effect is not known. Twenty-eight species of predators were listed in India but their effectiveness is not known (100). The reduviid *Platymeris laevicollis* feeds on *O. monoceros* adults in palm crowns in East Africa (64, 173) and attacked *O. rhinoceros* in cages. Although widely released in New Guinea, Western Samoa, Tonga, and Mauritius, there is no evidence that it became established (13, 121, 168), and perhaps the young nymphs were destroyed by ants. *Hypoaspis* sp. mites may destroy *Oryctes* eggs (168).

Nematodes

The nematode *Oryctonema genitalis* was described from the bursa copulatrix of females and the aedeagus of males of *O. monoceros* in the Ivory Coast. It reproduces in the bursa, may be transferred during beetle mating, feeds on spermatozoa, seminal fluid, and secretions of the bursal wall, and does not normally survive long outside the host. Its effect on the host and its reproduction are not known (143). Another nematode, *Rhabditis adenobia,* was described from the colleterial glands of *O. monoceros* females. It seems to have no injurious effect on the host and feeds on secretions and

bacteria (144). *Thelastoma pterygoton* was described from the intestine of *O. monoceros* and *O. boas* larvae in the Ivory Coast (145). Nematodes were found in the above organs of various *Oryctes* spp. in Madagascar (3) and in the bursa of *O. gnu* in Malaysia, *O. monoceros* in East Africa, and *O. centaurus* in Papua New Guinea (68).

Fungi

The use of the fungus *Metarrhizium anisopliae* against *O. rhinoceros* has been alternately in and out of favor since 1913. The history of its earlier use has been reviewed together with a discussion of a more recent field trial at Fagaloa Bay in Western Samoa (168). A low incidence occurred on *Oryctes* spp. in Madagascar (3, 116), Asia, and Africa (166, 191). On the southwest coast of India a high infestation occurred in the monsoon season (128) and it was prevalent in 1956 from May to October when humidity exceeded 70%, temperature was about 27°C, and the sky overcast more than 50% of the time (126). In 1964 a similar infestation occurred in Assam (100).

O. monoceros larvae all died after three weeks at 28°C in breeding medium infected with mild doses of *M. anisopliae* conidiospores (10^3 per g of medium). Temperature greatly influenced the development of the disease, which reached a maximum intensity between 25°C and 30°C. The humidity of the medium may or may not favor the infection. Only strains belonging to the major type (conidiospores measuring more than 9μ in length) and isolated from five *Oryctes* spp. were pathogenic to *O. monoceros* (32, 46). In India the long-spored (major) form was confined to *O. rhinoceros*, whereas short-spored forms occurred on other hosts. Only isolates from *O. rhinoceros* could infect *O. rhinoceros* (148). Although most insects studied are susceptible only to the strain isolated from the same species, *Oryctes* spp. larvae are susceptible to all the strains coming from several *Oryctes* spp. (47). More recently (43) it has been suggested that *O. rhinoceros* larvae are susceptible only to the strain isolated from this species. This is a somewhat different result from that obtained by Latch (94) who found that all long-spore isolates from *Oryctes* spp. were pathogenic to *O. rhinoceros* and that 23 short-spore (minor) cultures isolated from other insects caused lesions on *O. rhinoceros*, but only 5 were lethal. An isolate introduced into the field is unlikely to be more pathogenic than any of the long-spore strains already there. Only strains of major form that had been isolated from *Oryctes* spp. were pathogenic to *O. rhinoceros* adults. Half the adults died 75–80 days after spraying with 10 ml of suspension containing 1×10^5–1×10^6 spores/ml). Total mortality was obtained with concentrations of 1×10^7 spores/ml. A minor strain isolated from *O. rhinoceros* could develop saprophytically if a very concentrated spore inoculum was applied to a fresh *O. rhinoceros* cadaver (48). The fungus is mass produced saprophytically

on oat grains and can be applied as a microbial pesticide to the surface of breeding sites such as sawdust heaps. Three months after surface application most *O. rhinoceros* larvae are killed, and the spores remain viable in the breeding sites for at least 24 months (95). A filtrate from *M. anisopliae* altered the nucleus and cytoplasm of *O. rhinoceros* hemocytes in vitro and prevented their fusion and agglomeration (175). *Cordyceps* sp. killed up to 50% of *Oryctes* larvae in decaying logs on Isle Sainte Marie, Madagascar (3) but could not be bred in the laboratory.

Other Diseases

Surany (166) described "Heidenreich's watery disintegration disease" in which the larval fat body atrophies, hemolymph increases, the skin becomes translucent, and the larva moves to the surface of the medium to die. Although the disease could not be transmitted with techniques available at that time, a virus was suspected. It was especially noted at Medan, Sumatra, and Zanzibar, East Africa. Later the condition was thought to be an artifact due to unsuitable food (111). However it is now known that baculovirus does exist at Medan (191), so that Surany's conclusions regarding the viral nature of the disease there are probably correct. Marschall's (111) criticism may apply only to the Zanzibar material, since no virus has been reported in Africa and since Marschall worked only on the African *O. boas* and *O. monoceros.* Surany (166) also described "Maya's blue disease" in which the larva turns blue and dies over a period of hours. No causal agent was isolated, and it was believed (111) that an external trauma (e.g. the shock of a falling palm) caused rupture of one of the delicate gut diverticles, allowing the contents to ooze out into the hemolymph and causing the blue color to spread throughout the body. The condition can be produced artificially by throwing larvae hard onto the ground or by rough handling. Interestingly, "blue disease" was named a "controlling" factor in *Oryctes* populations in Madagascar (98) and the Philippines (42). In the latter case some symptoms described could have been due to baculovirus, now known to occur there (191).

Protozoan gregarine cysts have been observed in *Oryctes* spp. larvae and adults (3, 13, 71, 116, 172) but appear to have little adverse effect. A variety of diseases of the European *Melolontha melolontha* were not effective against *Oryctes* spp. larvae (79).

POPULATION FLUCTUATIONS AND POPULATION REGULATION

Collection of *O. boas* from crowns in the Ivory Coast showed marked regular fluctuations, with maximum catch in the dry season and minimum catch in the wet season, and a male/female sex ratio of 0.25 (105). Fluctua-

tions were similar on different plantations. The insect did not breed in decaying logs and so was unaffected by destruction of this wood. Fluctuations in *O. monoceros* numbers lacked the regularity and amplitude of *O. boas* and varied from plantation to plantation depending on alterations to breeding sites in the vicinity. All stages were present throughout the year, resulting in a complete overlap of generations. Sex ratio was 0.90 in crowns and 1.96 in breeding sites. On the same plantation there was no correspondence between population variations in the two species.

In New Britain the immigration rate of *O. rhinoceros* into blocks of 3–5 year-old coconuts showed no annual cycle or overall trend, but it was reduced by rain (8). Sex ratio was 0.91. The immigration rate of *Scapanes australis grossepunctatus* decreased with time (i.e. as the palms grew older) but was not affected by rain. Sex ratio was 3.69. The trend in the relative population size of *O. rhinoceros* at a plantation in New Britain with 10-year-old coconuts, high rainfall, and many breeding sites was studied (9) by using coconut "stump" traps to capture adults searching for breeding sites. The high initial population declined over the following three years, with the gradual disappearance of the breeding sites. Catches were somewhat higher at new moon but were depressed by rain. Sex ratio was 0.31, and all females were mated and had mature eggs in the lower ends of the oviducts. Adults of *S. quadrifoveatus* in Puerto Rico (142) were most abundant in June–July, but most stages were present throughout the year.

Natural enemies seem to have little effect in regulating *Oryctes* numbers. Many authors agree that the main determinant of *Oryctes* abundance is the number and availability of suitable breeding sites (3, 13, 27, 33, 56, 62, 66, 87, 109, 115, 116, 166). Overcrowding in breeding sites (33, 62), as well as density of palms available for feeding (27, 58, 121), may be an important factor.

METHODS OF CONTROL OTHER THAN BY BACULOVIRUS

Beetles have been traditionally removed from feeding holes in young palms with wires that are hooked or barbed at the end, but often only after damage has been done (21, 56, 114). They may also be cut from holes, but usually this causes more damage and the wounds attract more beetles or the secondary pest *Rhynchophorus*. Traps consisting of heaps of compost or wood (sometimes treated with *M. anisopliae*) (96, 99, 101, 142) or lengths of split palm log laid on the ground (27, 179) have been used but are laborious to set up and require frequent checking lest they themselves become breeding grounds (56). All authors are unanimous in advocating the destruction of breeding sites (e.g. 50, 56, 62, 73, 99, 103, 108, 114, 162); however the methods are laborious, expensive, unpopular, and frequently ignored. In

Western Samoa dead coconut trunks were dumped in the sea (20), whereas in Malaysia (24) and the Ivory Coast (23) the trunks were cut into lengths for stacking and burning. The problems in cutting and burning old oil palm stands in Malaysia have been described (179), and in Indonesia burying rather than burning trunks was suggested (96). Poisoning oil palms with arboricides prior to felling accelerates natural rotting (179). Grove sanitation reduced by 67% the loss of replanted palms due to *Strategus* attack (142). Many plantations in the South Pacific and Asia are overmature and should be felled and replanted. This has spurred interest in utilization of coconut trunks for timber and furniture-making (1, 49, 170), fence posts (49), and charcoal making in (49) small- and large-scale kilns.

A chemical screening program revealed that ethyl dihydrochrysanthemumate (chrislure) applied in metal vane traps was an effective attractant for *O. rhinoceros* (1a). When applied to the much cheaper coconut cap traps, more beetles were caught than in metal traps (5). Subsequently, the commercially available and cheaper ethyl chrysanthemumate (rhinolure) was found to be almost as effective (99a). However even with a high density of traps in a small area, many beetles do not enter the traps. Although useful in field surveys, the traps have not been developed to a stage where they can contribute to field control programs in the South Pacific because the cost of servicing them and vandalism are major drawbacks (49). Rhinolure with an olfactory reinforcer was tested against *O. monoceros* in the Ivory Coast with 4 traps/hectare. More beetles were caught by traps at the plantation borders and when the breeding sites were covered by vegetation; in the latter case the traps apparently imitate the odors of natural breeding sites (90).

O. rhinoceros was eradicated from Niuatoputapu Island by destruction of the insects and breeding sites over a seven-year period ending in 1930 (20, 159, 161), but this would be uneconomic nowadays. Eradication was attempted at two islands in Fiji. Some 506 coconut cap rhinolure traps were operated on Vomo (109 hectares) and 317 traps on Bekana (16 hectares); from December 1971 to the end of February 1974, 3644 beetles (1626 males, 2018 females) were removed from Vomo and 2462 from Bekana (1082 males, 1380 females). Destruction of breeding sites and larvae was done concurrently (18, 19), and palm damage declined. However as there remained a low but persistent population which could not be trapped, it appeared that possible results from the indefinite continuation of the trial were no longer commensurate with the costs, and the trial ended in late February 1974. Insecticides such as 90% lindane granules mixed with sawdust (104, 108) or a mixture of 1 part gamma benzene hexachloride (50% wettable powder): 9 parts damp sawdust (125, 132) may be placed in the axils of the youngest 4–5 fronds, but this is labor-intensive. The same

problem applies to the pouring of dieldrin into holes drilled at one meter intervals along old oil palm trunks to prevent development of larvae (110).

Owen (137) suggested that vegetative barriers could interfere with the beetle's perception of palm crowns sought for feeding, conceal breeding sites, and provide a physical barrier to flight since they are clumsy fliers. In an experiment in Malaysia where *O. rhinoceros* was breeding in rubber logs, eleven months after establishment of a bare ground plot, all stages except eggs totalled 52.5/0.40 hectare in bare ground and 9.3/0.40 hectare under dense legume cover, and they were more common under sparse than under heavy cover. Three months after establishment, the incidence of severely damaged palms was 28.4%, 9.4%, and 2.0%, and the incidence of undamaged palms was 35.4%, 48.7%, and 69.9%, on bare ground, with sparse cover, and with dense cover, respectively (180). Similar results were found when rotting oil palm trunks were covered with dense ground vegetation (181). Thus breeding is restricted, frequency of attack on young palms is reduced, and the logs can be left lying flat in situ. The cover provides an effective and inexpensive means of controlling the pest during the critical early period of palm replanting. In the Ivory Coast the legume *Pueraria javanica* was used to cover windrows of forest wood 7–9 months after felling and greatly reduced attacks on young coconuts (88).

Adult *O. rhinoceros* males were sterilized by a gamma ray dose of 10,000 rads. The ratio of irradiated males to normals must be greater than 10:1 to have any marked effect on egg fertility (77), and this could militate against any sterile male release plan. Nine alkylating agents, derivatives of aziridine, had a sterilizing effect on males but tended to reduce their longevity and thereby reduced their competitiveness compared to normals. Tepa did not stop formation of mobile spermatozoa, but eggs laid by females that had mated with treated males ceased development at an early stage (78). A number of juvenile hormone mimics were shown to have an effect when applied topically or injected into young *O. rhinoceros* pupae. The most effective was methoprene (31).

USE OF BACULOVIRUS

Readers are referred to a forthcoming review for a more detailed treatment of this topic (17). The virus was first discovered in *O. rhinoceros* larvae in Malaysia and named *Rhabdionvirus oryctes* (69, 70). It has since been found throughout the Philippines, Sumatra, and west Kalimantan (191). It did not exist in any South Pacific countries. It was first observed in nuclei of larval fat body cells (69). Later it was found in nuclei of midgut epithelium of larvae and adults (72, 140) and also in the adult ovarian sheath and spermatheca (117). It multiplies in nuclei of cultured larval *O. rhinoceros* heart

and blood cells (147) and moth (*Spodoptera frugiperda*) and mosquito (*Aedes albopictus*) cells (92). The structure of the virions (119, 140, 141, 153) indicates that it belongs to the baculovirus group. In infected larvae the abdomen becomes turgid and glassy, the fat body disintegrates, and the amount of hemolymph increases, so that the larvae appear translucent when viewed against light. Internal turgor may increase, extroverting the rectum. In the terminal phase chalky white bodies may appear under the abdominal integument (69). Much virus multiplication occurs in the midgut epithelium (140).

The lethal infection time for larvae that have eaten virus-contaminated medium depends on the instar: first instar larvae die after 9 days, second instar after 13 days, and third instar after about 23 days. Given similar doses by force-feeding, young third instar larvae died after 18 days, and old ones after 25 days (184). High temperatures speeded death (32°C compared with 25 or 27°C). The virus also killed second or early third instar larvae of *S. a. grossepunctatus* within 13–15 days of infection, but some older larvae seemed to be resistant (4). In the Ivory Coast, larvae of *O. boas* showed a sensitivity to the virus that was similar to that of *O. rhinoceros* larvae, but *O. monoceros* larvae were much less susceptible, so field trials were not undertaken (89). In the Philippines several strains of baculovirus were found in *O. rhinoceros* that differed in their pathogenic effects; some seemed to infect larvae more easily than the strain that originated in Malaysia and was introduced to the South Pacific. Differences were also noted in the survival times of larvae after inoculation with different Philippine strains (191).

In adults virus multiplies in nuclei of midgut epithelial cells, and the gut eventually fills with disintegrating cells and virus particles (72, 120). Infected adults defecate virus into the surrounding medium (185). Thus adults are virus reservoirs, spreading infective virus into the insect's natural habitats (72). Up to 0.3 mg virus/day may be produced in the feces of an infected adult (118). Diseased beetles generally show no external symptoms, but in virus-treated breeding sites Monty (120) found nine beetles with malformed elytra, wings, or abdominal wall, and one of the beetles contained virus. However Zelazny (189) believes that virus is not normally carried over in development from the infected larva to the adult stage. In the laboratory, infected adults died sooner (25 compared with 70 days) and laid fewer eggs than healthy controls (1.25 ± 0.13 compared with 14.7 ± 1.5 eggs/female) (185).

Virus is mass produced by feeding batches of healthy larvae on medium mixed with macerated virus-killed *O. rhinoceros* larvae. The virus-packed cadavers are removed daily and are deep-frozen for indefinite storage (11, 182). Storage of virus as macerated cadavers mixed in sawdust at 26°C reduced viral activity to 0.091% of its initial value in one week and to

0.027% in two weeks; no activity was detectable after one month. Drying or warming increased the rate of inactivation (184). Safety testing with purified virus (49) showed no pathogenicity to eight tissue cultures (two human and two pig cell cultures, and one each from mouse, hamster, fish, and calf) or to various organs of mice up to 60 days after inoculation. In laboratory studies (189) *O. rhinoceros* adults became infected per os in a mixture of sawdust and macerated virus-killed larvae, or when kept together with virus-infected adults. Adults developing from larvae that had survived exposure to various dosages of virus were not infected, nor were larvae hatching from eggs that had been surface-contaminated with virus. Larvae hatching from eggs laid by infected females rarely were infected. Nevertheless, in adults virions have been found in the nucleus and cytoplasm of spermatids, in cells and lumens of accessory glands, and in the ejaculatory canal, as well as in chorionated oocytes and follicle cells (116a). In *O. rhinoceros* populations the virus is transmitted most frequently during mating, possibly when the healthy partner contacts by mouth the virus that has been defecated by the infected partner. It can be similarly transmitted when infected and healthy beetles feed together in palms. Beetles visiting larval breeding sites that contain freshly virus-killed larvae can become infected, and such beetles pass the infection to healthy larvae when visiting another breeding site (189).

Three methods of applying virus have been used, each superseded by the subsequent one as the mode of transmission became more clearly understood. The first method involved placing up to 50 macerated virus-killed larvae in an artificial compost heap, which was then visited by beetles that became infected as they crawled through it. Later they flew away and spread virus elsewhere. These heaps had several disadvantages (11). Another method was to place virus-killed larvae and live infected ones under 6–10 one meter lengths of split coconut log, but disadvantages persisted (11). Finally it was found that the simplest, most economical, and most direct method of virus dissemination was to release laboratory-infected beetles, a method introduced early in 1972. Beetles are immersed for 2–3 min in a suspension of 2 macerated cadavers/liter of water, then allowed to crawl for 24 hours through about 1 kg of sterilized sawdust mixed with half a virus grub in 500 cm^3 of water. Zelazny (190) obtained 90% infection by forcing beetles to swim for 10 min in a 10% suspension of macerated freshly virus-killed larvae. Beetles were allowed to crawl under logs or into vegetation and fly off at night. Dispersing widely before death, the beetles spread the disease directly into the wild population, and contaminated breeding sites that contained larval broods and other beetles as well as palm crowns.

Beetles used for testing may be caught in attractant traps, and breeding sites may be searched for live or freshly dead *Oryctes* material. Virus may be detected by the following methods: electron microscope observation of

virions in infected feces (118), histological examination (72, 120), immuno-logical testing (26), bioassay method (184), adult midgut-content smear (49), and macroscopic examination of the adult midgut (49).

Introduced into artificial log heaps in Western Samoa in 1967, the virus became established in the *O. rhinoceros* population in one year and spread to other parts of the islands (112). It apparently reduced the beetle popula-tion considerably. However, lack of quantitative damage surveys caused certain doubts and questions that stimulated work elsewhere. In 1969, 73% of larvae collected from natural breeding sites died of virus. However, it is now known that the larvae were bulk-collected and cross contamination occurred. As a result, findings did not represent the mortality in the wild population (168); however they sufficed to show that the virus was estab-lished. Careful studies in 1970–1971 showed that in fact only about 3% of larvae and 35% of adults in the wild were infected, and a mean of 7.3% of breeding sites contained infected insects (186). Larval breeding sites were most likely to contain infected insects if the sites bore two broods instead of one, and if breeding was extensive in the area. Sites were less frequently visited by infected than by healthy females. Mated females collected from palms were more often infected than egg-laying females from breeding sites. Infections in males increased with age, but young females were more often infected than very young or old females (186). From 1971 to 1974 breeding sites with infected larvae fluctuated between 5.6 and 11.2% (average 8.2%) (190). Detailed surveys showed that the pattern of 12.5 to 18% of fronds damaged seemed to follow these fluctuations most of the time. Between 1973 and 1975 the percentage of infected beetles in traps fell from 63 to 35% (average 51%), which coincided with a significant decline in the number of beetles trapped. More males than females were found to be infected.

In Fiji virus application began in 1970 using the three methods as they evolved (11, 15). Sampling in 1971–1972 showed that on the islands of Beqa and Vatulele 2–3% of breeding sites contained infected specimens. On the main island of Viti Levu, the proportions of beetles found infected were 68% at Suva from January to March 1974, 66% between Lautoka and Nadi from September 1973 to March 1974, and 57% at Caboni from June 1973 to February 1974. Trappings on numerous other islands showed that the virus was established, and surveys before release and at later intervals showed that in many localities damage fell significantly 12 to 18 months after virus establishment (Figure 1). On Wallis Island virus was applied in artificial log heaps from September 1970 to June 1971. Less than two months after the program began, virus had spread over the whole island (57) and in one year the adult beetle population fell by 60–80% (59). The percentage of fronds damaged fell by an average of 82%, ranging from 90% in densely planted groves to 76% in more open groves.

Virus was released into artificial sawdust heaps and log heaps on the western tip of Tongatapu, Tonga between November 1970 and January 1971 (182). The epizootic spread about 3 km/month. Breeding sites with infected *O. rhinoceros* ranged from 2 to 40%, depending on time elapsed since release and on distance from the release point. Behind the zone of spread, the virus incidence fell again. In the release zone rapid damage surveys showed that the palms had noticeably improved at 350 days postin-troduction of virus; according to the known rate of frond replacement, a significant change in beetle numbers must have occurred at about 200 days postintroduction. In the release zone, the number of palms with central crown damage fell from 28% at 150 days postintroduction to 5% at 455 days, and in the next zone of spread from 27% to 10%. In American Samoa virus-infected beetles were released at one site in early 1972 (49) and dam-age declined as the virus spread at 0.8–1.6 km/month. The further the locations were from the release point, the later was the decline in damage (187).

Virus was introduced to the Tokelau Islands in artificial log heaps in 1967. An experiment to observe the effect of additional virus application was
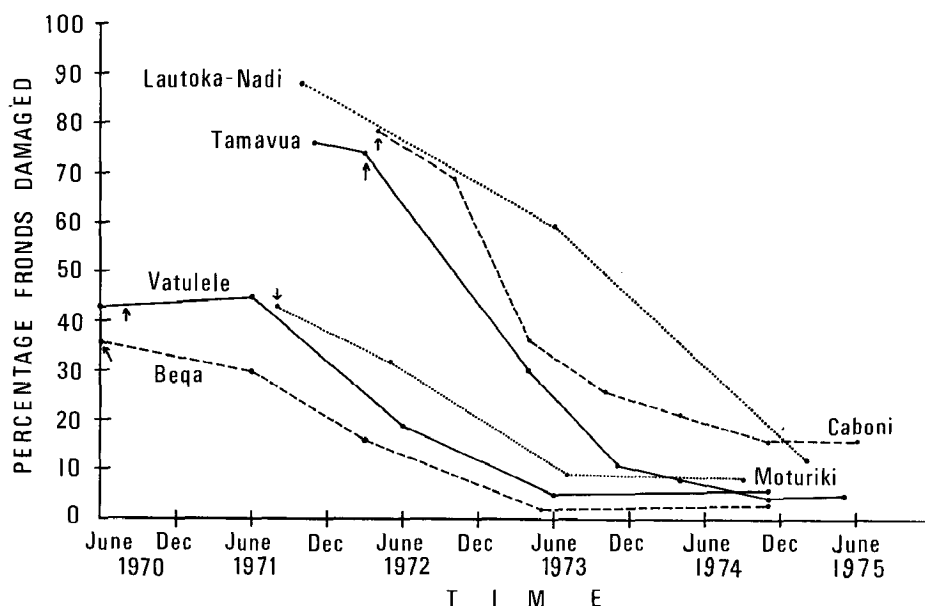

Figure 1 Effect of baculovirus on palm damage by *Oryctes rhinoceros* at localities in the Fiji Islands. Arrows indicate time of virus introduction. Virus had spread naturally into the Lautoka-Nadi area by mid-1973.

begun in January 1973 (190). The islets of Nukunonu atoll, which lie in an ellipse 8 X 13 km, were divided into two treatment groups and one control group. No treatment was applied to the east and west control islets, which separated the treated north (90 hectares) and south (40 hectares) by 10.5 km to the east and 4.5 km to the west. On both treated groups of islets beetles were caught with attractant traps and larvae were collected every 2–3 months. Female beetles and larvae were killed, but male beetles were returned to the south islets in groups of 20/week after injection with hemolymph from infected larvae. The program continued for 20 months; damage to 1000 marked palms was recorded initially and after 23 months. On the control islets, damage increased slightly. On those with beetle traps and larval collections, the number of beetles trapped fell from 240 to 149/month, and the number of upper fronds damaged fell slightly from 3.7 to 2.4%. On the islets where additional virus application as well as trapping and larval collection took place, reduction in the number of beetles trapped was significantly more pronounced (from 82 to 14 beetles/month); the decline started after 10 months, proportionately fewer females were trapped, and damage was significantly reduced (6.5 to 1.9% damaged fronds).

Virus applied in manure heaps in Mauritius from 1970 to 1972 (121) reduced the average number of larvae per heap from 24.6 in 1970 to 4.6. in 1976–1977. Infected larvae were found in dead standing palms, indicating transmission by adults. No more virus was released after 1972. Damage to palms was reduced by 60–95% (58). Now that the beetle population is regulated by virus, perhaps the main way that damage could be further reduced would be to decrease the beetles/palm ratio by increasing the overall number of palms through replanting.

CONCLUDING REMARKS AND SUGGESTIONS FOR FURTHER WORK

Further work should be undertaken on the effects of beetle attacks on coconut production in palms of different ages, growing in different climates and on soils of differing fertility. Virus can assume an important, even primary role in integrated control programs, as it is successful and very attractive economically. It can be used in conjunction with cover crops to conceal breeding sites, or coconut timber utilization to reduce the number of sites. *M. anisopliae* spores can be applied as a microbial pesticide to large sawdust heaps around sawmills. As virus is soon inactivated, it can persist in an area only if some natural breeding sites and an adequate *O. rhinoceros* population remain to propagate and transmit it.

Because Malysia was the source of the virus, it would be of interest to map its distribution and incidence in that country and its correlation with

beetle populations and damage levels. Strains of the virus might be useful in field releases against *S. australis,* and it could be tested on other *Oryctes* species such as *O. gnu, O. centaurus,* and the date pest *O. elegans,* as well as *Papuana* and *Strategus* species. If an unusually large number of breeding sites is created locally, e.g. by felling of palms, the *O. rhinoceros* population can resurge in these "outbreak" areas and increase damage to neighboring palms despite the virus. Long-term investigations should examine the value of repeated releases of virus-infected beetles in the outbreak areas as was done in Tokelau (190). The islets of Nukunonu are small and isolated, but on large islands or land masses released beetles could disperse from the outbreak areas, thus diluting their effect. There is as yet no evidence that *O. rhinoceros* populations in the South Pacific are developing resistance to the virus, but this possibility should be monitored. New virus strains may need to be introduced.

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