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OBSERVATIONS ON THE BIOLOGY AND ECOLOGY OF *ORYCTES RHINOCEROS* AND *SCAPANES AUSTRALIS* (COLEOPTERA: SCARABAEIDAE: DYNASTINAE): PESTS OF COCONUT PALMS IN MELANESIA

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Abstract

Marked biological and ecological differences are reported between the coconut palm rhinoceros beetles *Oryctes rhinoceros* and *Scapanes australis* in Papua New Guinea. Differences of distribution, preferred breeding site, age group of palm attacked, and duration of the immature stages, are such that no competition for resources occurs between the two species. Damage to palms varies greatly from one locality to the other. Natural enemies appear to be of little importance, the number of suitable breeding sites limiting the abundance of these dynastines. Methods for insectary breeding of the two species are described.

Introduction

Oryctes rhinoceros L. is an important pest of the coconut palm. It occurs from India and Ceylon eastwards throughout south east Asia, and has also been accidentally introduced into a number of South Pacific islands (Catley 1969). *Scapanes australis* Boisduval is restricted to Papua New Guinea and the Solomon Islands. Although *O. rhinoceros* is well known from other areas, few details were previously available on its biology in New Guinea, while the life history of *S. australis* was unknown. It had been assumed that in localities where the two species co-existed (such as the Gazelle Peninsula of New Britain), there would be competition between them for resources. In the present work the biology and ecology of the two species have been critically examined and compared with a view to assessing the relative importance of these pests in new and established coconut plantations in the Melanesian region.

Throughout this paper the abbreviations L1, L2 and L3 are used to denote first, second and third instar larvae respectively. Descriptions of dynastine larvae associated with coconut palms have been given by Bedford (1974). Most localities mentioned in the text are shown in Fig. 1.

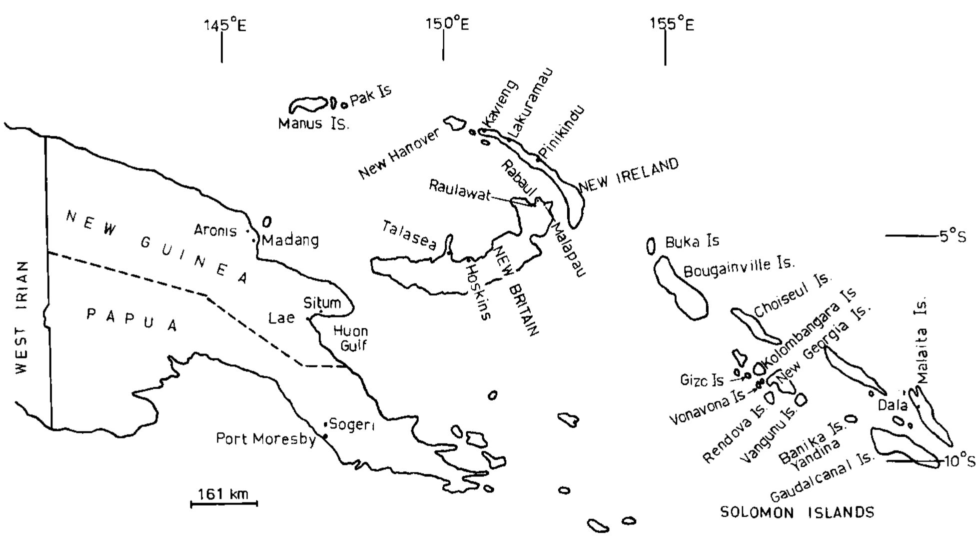

FIG. 1.—Map of Papua New Guinea showing most localities mentioned in the text.

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Oryctes rhinoceros

Distribution in Papua New Guinea

O. rhinoceros reached New Britain about 1942, and subsequently was reported from New Ireland (1952), West Irian (date unknown), Pak Is. (1960) (Catley 1969), and Manus Is. (1970). In New Britain it is apparently restricted to the Gazelle Peninsula, and has not been found in the West New Britain area (Cape Hoskins-Stettin Bay-Talasea). Neither has it spread to the New Guinea or Papua mainland, Bougainville or the Solomon Islands.

The lack of spread of *O. rhinoceros* within Papua New Guinea, despite frequent air and shipping connections, occurrence of conditions favourable for its establishment, and absence of consistently applied quarantine measures against it, is in marked contrast to what occurred in the Fiji group, where it has spread, despite costly quarantine measures, from Viti Levu to 41 other islands since 1960.

Breeding Sites

Dead standing palms.—These are the most favoured breeding sites for *O. rhinoceros*. Palms may die from old age, or waterlogging, or sometimes a group of 10 to 20 palms in a plantation may be killed by a lightning strike. Some 129 of 159 dead standing palms felled and examined at various sites in the Gazelle Peninsula and New Ireland during 1968 and 1969 had *O. rhinoceros* material in their tops; the L3 stage predominated in 74% of the sites. To assess the occurrence of various developmental stages of *O. rhinoceros* in the tops of dead standing palms at different times of the year, samples of 6 to 7 suitable trees scattered through the large planting at Malapau, Gazelle Peninsula, were felled at one or two month intervals from October 1968 to November 1970. The numbers of all *O. rhinoceros* stages present were recorded; the results averaged, for each month of the year, are shown in Fig. 2.

This size of sample sometimes proved inadequate when one or two of the palms felled contained no *O. rhinoceros* material. On rare occasions one palm in a sample contained a large proportion of a shortlived stage (such as the egg, L1 or L2) and this tended to skew the sample. However, it was not possible to take larger samples of palms without risking disruption of the ecosystem for the beetle in the area, and without unduly depleting those available for later samplings. Despite this, however, it became clear that the L3 stage predominated throughout the year (excepting April and July) and ranged from 25 to 90% of stages present. This is understandable since the L3 is the longest developmental stage in the life history. Oviposition peaks occurred in February-April and September-October. Some palms contained a number of L3, and also eggs or L1, indicating that different broods (at different developmental stages) were present.

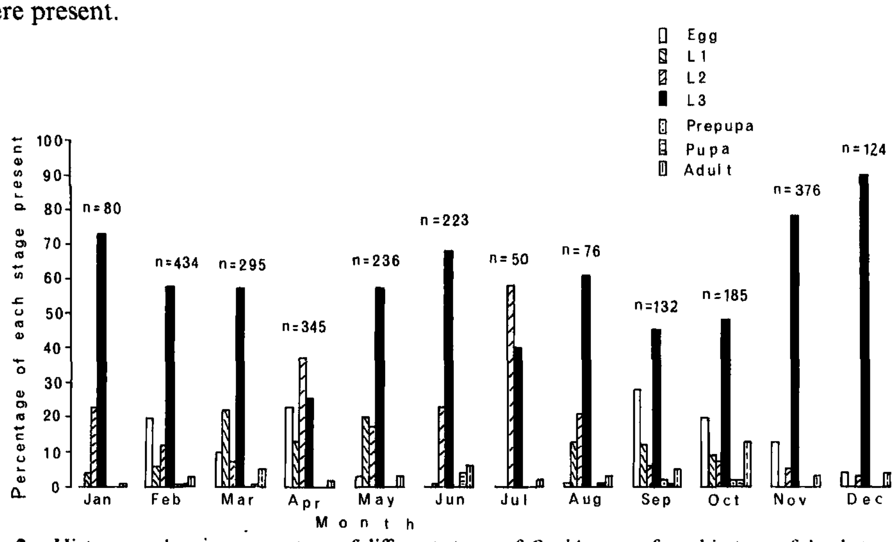

FIG. 2.—Histogram showing percentage of different stages of *O. rhinoceros* found in tops of dead standing palms at Malapau during the year. (n = total of all stages.)

Dead coconut trunks and stumps.—These frequently served as breeding sites. Decaying trunks examined at Lakuramau revealed breeding in the ends but not in the rest of the trunk. At Raulawat, freshly dead stumps of younger palms sometimes contained larvae of the palm weevil *Rhynchophorus bilineatus* Montrouzier, as well as those of *O. rhinoceros.*

Decaying cocoa pod humus.—Sampling of the black humus beneath extensive heaps of decaying cocoa pod husks at Pinikindu Plantation, New Ireland, on 20 June 1968, revealed 20 L3 and one L2 in about 0.1 cu.m. Although similar heaps were examined in other parts of New Ireland and the Gazelle Peninsula, no further instances of *O. rhinoceros* breeding were detected.

Feeding Sites and a Survey of Damage

Damage at a given locality was usually assessed as the proportion of affected palms in a stand, but in some cases more detailed surveys involved counting the number of damaged fronds on each palm.

On coconut palm.—*O. rhinoceros* attacks the palm by flying to the central crown and crawling down an axil of one of the younger fronds until it reaches the stem where it begins to bore in to feed. In New Britain and New Ireland it was found to attack mainly palms that were already several years of age (Fig. 3) and was rarely found on very young, post-seedling palms or those up to two or three years of age. Gressitt (1953) made similar observations in the Palau Islands. The percentage of palms attacked varied widely from one locality to another, ranging from 0 to 100.

On oil palm.—At two localities (Lowlands Agricultural Experiment Station, Keravat, New Britain, and Tigak Agricultural Station, New Ireland) light beetle damage attributed to *O. rhinoceros* and consisting of holes in frond bases, was found on tall oil palms. Although no beetles were found, it is considered that this species was responsible, because of the height of the palms (*cf.* section on *S. australis* feeding sites).

Life Cycle and Oviposition

All observations were made in an insectary at Keravat, the diurnal temperature of which ranged from 21 to 35° C.

Breeding method.—One male and one female beetle were confined together in a wooden box of dimensions 18 × 18 × 25 cm. The lid was a wooden frame covered with strong wire mesh. The box was two-thirds filled with rotted sawdust as the oviposition medium. Three pieces of sugar cane were placed on the surface as food for the adults and were renewed twice weekly.

For duration of life history studies the boxes were emptied daily, and the medium examined for eggs, which were carefully removed with forceps and placed individually in small circular plastic pill boxes 5 cm in diameter and 2.5 cm high. On hatching the young larvae were reared individually in 2.5 *l* tins, each about half full with a 1:1 mixture of cowdung and sawdust which had earlier been allowed to ferment. Such a medium had previously been advocated by Hurpin and Fresneau (1967) for rearing dynastine larvae, for under these conditions epizootics of the green muscardine fungus *Metarrhizium anisopliae* (Metsch. (Sorokin)) rarely occurred, any spores originally present having been killed by heat generated by fermentation in the mixture prior to its use.

The larval food medium was replaced every 3 to 4 weeks during the early stages of development, and every 2 to 3 weeks during the third instar. The tins were checked daily for signs of moulting or pupal cocoon construction. When preparing to pupate, larvae compacted most of the available medium to form a pupal cell; such larvae were allowed to remain undisturbed until the emergence of the adults.

Duration of the life cycle.—The duration of the immature stages of *O. rhinoceros* under Keravat conditions is shown in Table 1, while the results of various authors are presented in Table 2. From a comparison of these sets of results it appears that the duration of the third larval stage was shorter under the Keravat rearing conditions.

TABLE 1

DURATION OF IMMATURE STAGES OF *O. RHINOCEROS* AT KERAVAT, NEW BRITAIN

Stage	Numbers of specimens studied	Duration (mean days) (± 95% C.L.)	Range (days)
Egg	30	12 ± 0.4	8–13
L1	31	16 ± 0.4	14–19
L2	24	19 ± 1.1	15–22
L3	26	60 ± 3.1	51–73
Prepupa	19	13 ± 0.8	10–15
Pupa	19	22 ± 1.3	13–25
Total		142	

TABLE 2

DURATION OF THE DIFFERENT STAGES OF *O. RHINOCEROS* ACCORDING TO VARIOUS AUTHORS, AND A COMPARISON WITH RESULTS OBTAINED AT KERAVAT

Authors and date	Egg (days)	L1 (days)	L2 (days)	L3 (days)	Pupa (days)	Adult (months)	Total (months)
Mackie 1918	10–12		120–150*		28		
Leefmans 1920	12		60–120*		19–27	4–4½	7–10
Friederichs & Demandt 1922	10–12		300*		20		
Cherian & Antananarayan 1939	9–14		105–180*		25–40	3½–7½	8–15
Gressitt 1953	11–13	19	21	39	16–24	2–4	5–9
Goonewardene 1958	7–12	15	18	85	18	3	8
Kurian & Pillai 1964	10		90–180*		20	2½–7	6½–14
Hurpin & Fresneau 1967	8	10	12	165	26	4	11½
Catley 1969	12	10–14	12–18	90–120	23–28 (plus 8 as prepupa)	up to 6	
Bedford (from Table 1)	12	16	19	60	22 (plus 13 as prepupa)	6–9	11–14

*total duration, L1, L2, L3.

Fecundity.—Six reared pairs (♂, ♀) of *O. rhinoceros* were confined in wooden boxes of the cowdung/sawdust mixture until oviposition ceased. The boxes were emptied weekly and the contents examined for eggs, which were removed and counted before the insects were replaced. If a male died, a replacement was added.

Egg production per female ranged from 24 to 65, with a mean of 51 ± 16 (95% confidence limits calculated from t distribution since $n < 30$). This mean agrees well with the 49 eggs per female reported by Hurpin and Fresneau (1967).

Adult longevity.—The mean total adult life for five females was 274 ± 41 d (95% c.l. from t distribution). For six males the mean total adult life was 192 ± 26 d (95% c.l. from t).

This represents a mean adult life of 6.4 months for males and 9.1 months for females. Hurpin and Fresneau (1967) reported an average adult life for both sexes of about 4 months, with a range of 1 to 8 months.

Scapanes australis

Distribution

Males of *S. australis* show considerable variation in the size of the horns. Endrödi (1957) recognised four geographic subspecies based on the following characters of adult males with large horns: body size, degree of elytral puncturation, and shape of pronotal and head horns. *S.a. australis* Boisduval occurs on the New Guinea mainland west of the Huon Gulf, and *S.a. brevicornis* Sternberg east of the Gulf; *S.a. grossepunctatus* Sternberg on New Britain and New Ireland, and *S.a. salomonensis* Sternberg on Bougainville and the Solomons. In the Solomons, *S.a. salomonensis* is found on the islands of Guadalcanal, Malaita, Vonavona (Parara), Kohinggo (Arundel), New Georgia, Rendova, Vangunu and Kolombangara, but not on Banika or Gizo Islands.

Breeding Sites

There has been considerable confusion in the literature concerning the breeding sites of *Scapanes*, many authors assuming them to be identical with those of *O. rhinoceros* (Preuss 1911, Pagden and Lever 1935, Lepesme et al 1947, Simon-Thomas 1960, Smee 1965, O'Connor 1969). The present work has shown this assumption to be invalid and has now established that *Scapanes* breeds under the decaying trunks and stumps of bush trees.

Eleven *S.a. australis* larvae were found at the soil surface under decaying logs (not coconut) at Situm Land Settlement Scheme (east New Guinea mainland). Some were facing cavities which they had hollowed into the wood, and these cavities often contained chewed wood and faecal pellets. Where more than one larva occurred under a single log, they were well separated from each other. Four L3 were found in separate tunnels filled with faecal pellets in the base of a decayed sago palm stump at Aronis near Madang. The identity of these latter larvae was confirmed by rearing.

Seven L3 of *S.a. salomonensis* were found in the soil associated with the roots of a decaying bush stump at Dala Agricultural Station on Malaita Is. in the Solomons, and

FIGS. 3-7.—**(3)** palm damaged by *Oryctes rhinoceros*; **(4)** young palm damaged by *Scapanes australis* (note V-cut fronds); **(5)** *Scapanes australis* hole with chewed fibre in lower part of trunk of young palm; **(6)** young palm with fronds twisted and compressed due to *Scapanes australis* attack; **(7)** *Scapanes australis grossepunctatus* pupa.

one L3 was found under a decaying trunk at the soil surface facing a cavity chewed in the trunk.

Three *S.a. grossepunctatus* L3 were found in the rotting moist humus beneath heaps of decaying broken cocoa pods at Napapa No. 4 Village on the Gazelle Peninsula.

Feeding Sites and a Survey of Damage

On coconut palms.—*S. australis* appeared to restrict its attacks to young palms, from just past the seedling stage up to about five years of age (Fig. 4). The beetles either crawled down an axil before boring into the heart of the stem, or bored straight into the trunk from the outside (Fig. 5). Because it readily attacks very young palms which cannot sustain much damage, this species is a more serious pest than *O. rhinoceros*. Such attack was observed on 1½-year old palms at Daebangara on Kolombangara Is. in the Solomons, where many of the palms were holed and killed. Often more than one beetle occurred in the same hole, and females were usually deeper inside than males.

Sometimes the growing point was not completely destroyed by the beetle, but the young palm was always more or less deformed, producing twisted fronds with the leaflets compressed and crumpled together (Fig. 6). Palms a little older which received serious damage often had the inner fronds invaded by termites and mealybugs. As with *O. rhinoceros*, the incidence of *S. australis* varied greatly from one locality to another, varying from 0 to 100% of palms attacked.

Gressitt (1953) observed that in Western Samoa an abundance of undergrowth in village coconut groves could protect young palms against *O. rhinoceros* by interfering with adult flight. However, this was not always the case with *S. australis*. A three-year palm in a small planting at Munda, New Georgia Is., British Solomons, was completely surrounded by undergrowth higher than the palms, yet two male and one female *S. australis* occurred in one hole in the basal part of the trunk 25 cm up from the ground. Another case occurred in a garden of young coconuts at Patupaele on Kolombangara Is., Solomons, where a 2½-year old palm was partially hidden and surrounded by high growing cassava foliage, yet a male *S. australis* was found in a hole in the trunk.

On oil palms.—*S. australis* also attacked young oil palms. Damage took the form of holes in the frond base, midribs of fronds chewed through, ends of fronds V-cut, and stunting and twisting of the growing point sideways with the leaflets of emerging fronds compressed and deformed. In a few cases the young palm was killed. This was noticed at the large oil palm development scheme in the Cape Hoskins area of West New Britain. When surveyed in January 1970, the oil palms were about two years old. The original forests had been felled, and the large trunks had been allowed to remain in situ, but a dense cover crop of *Pueraria phaseoloides* Benth. had been planted as a "vegetative barrier" (*c.f.* Wood (1968)) with the objective of concealing the logs from rhinoceros beetles searching for breeding sites or hampering the movements of beetles to them. Overall, damage was very light. Attack was noticeably more frequent on palms near the edge of the planting (i.e. close to the bush), than in its centre. However, despite much searching, no *S. australis* could be found breeding in the bush and forest, which appeared to offer few suitable breeding sites and, in any case, severely hindered free flight. Searches were also made for larvae in the planted areas, but none were found under logs that could be moved. It seems likely that beetles existed in the forest before felling and that they may develop in small numbers within the planted areas under logs which have not yet been completely covered by *Pueraria*. Beetles apparently fly out from such breeding sites to reach the edge of the forest which they seldom penetrate, and are then deflected back into the open planted areas of young oil palms, the edge rows of which are then preferentially attacked.

On banana plants.—Szent-Ivany and Barrett (1956) reported that *S.a. grossepunctatus* adults had been found boring into the stems of banana plants at Keravat, New Britain, and that *S.a. australis* had been found near Sogeri, Papua, attacking isolated bananas in secondary bush adjoining forest.

Adults of both sexes of *S.a. grossepunctatus* were observed attacking stems of banana plants in the Gazelle Peninsula. *S.a. salomonensis* caused similar damage to bananas on Vonavona Is. and Kolombangara Is. in the Solomons.

On forest palms.—Wild palms (e.g. wild betel nut (*Areca* sp.) and "limbon" palms (either *Gulubia costata* Becc. or *Caryota rumphiana* Mart.)) form only a small proportion of native forest trees and, therefore, probably support only low populations of *S. australis*. Certainly, no example of damage by this species was apparent in the few forest palms that were examined.

Life Cycle and Oviposition

Breeding methods.—Considerable difficulty was experienced at first in inducing *S.a. grossepunctatus* to lay eggs. Trials of the *O. rhinoceros* oviposition medium and other media based upon rotted sawdust and compost proved unsuccessful, and it was ultimately established that *S.a. grossepunctatus* would oviposit only in black soil. Oviposition studies with this medium were conducted in wooden boxes as described for *O. rhinoceros*. Eggs were mainly deposited at the bottom of the boxes, and each egg was encased in a little spherical ball of compacted soil. The internal cavity of the ball was smooth-walled and somewhat larger than the egg.

Eggs, when new laid, were elliptical in shape, measuring 4.75-5.80 mm in length (average 5.18 mm, n = 7) and 2.95-3.25 mm in width (average 3.14 mm). Such eggs were very sensitive to desiccation, and quickly shrank and burst if exposed to excessive heat or dryness. During incubation the eggs enlarged and tended to become more rounded in shape. Mature eggs were 4.30-5.95 mm long (average 5.20 mm, n = 15) and 4.0-4.90 mm wide (average 4.40 mm).

Eggs were removed from the oviposition medium and transferred to small plastic pill boxes of cowdung/sawdust medium for incubation. Mortalities were high, and of a total of 2023 eggs laid between December 1969 and August 1970, only 18% hatched, while the remainder rotted. The reason for this loss is not known. On hatching, larvae were transferred to individual 2.5 *l* tins of cowdung/sawdust, which proved a most satisfactory rearing medium. It was renewed every 3 to 4 weeks for the younger stages, and about every two weeks for the third instar larvae. The weights of 10 well-fed third instar larvae ranged from 21.7 to 35.1 g (average 28.2 g).

Prior to pupation a larva compacted all the medium in its tin to form the pupal chamber, presumably by application of some secretion. When such compaction was noticed, no further change of medium or disturbance was made. Progress of pupal development was monitored by shining a torch through a small observation hole carefully broken through the pupal chamber to the cavity within. The hole was closed with a cover of moistened blotting paper when not in use. The interior of the pupal chamber was smooth walled and quite roomy, considerably larger than the pupa itself. The pupa is shown in Fig. 7.

Duration of the life cycle.—The duration of the immature stages is shown in Table 3.

Fecundity.—Egg production was studied essentially as described for *O. rhinoceros*, but black soil was used as the oviposition medium. In all, 52 pairs were set up. Supplies of reared males were limited, and mortalities were, therefore, sometimes made good with

TABLE 3

DURATION OF IMMATURE STAGES OF *SCAPANES AUSTRALIS GROSSEPUNCTATUS* AT KERAVAT, NEW BRITAIN, AND A COMPARISON WITH *ORYCTES RHINOCEROS*

Stages	No. of specimens	Mean duration in days (and 95% C.L.)	Range (days)	Mean duration in days for *O. rhinoceros*
Egg	31	32 ± 1	28- 38	12
L1	31	35 ± 1	21- 42	16
L2	31	45 ± 2	36- 61	19
L3	37	190 ± 8	140-253	60
Total larval life		270	197-356	95
Prepupa	33	21 ± 1	15- 30	13
Pupa	31	45 ± 2	33- 55	22
Total Immature stages		368	273-479	142

field-collected material. In three such cases the replacement males subsequently proved to be infected with *M. anisopliae* and they, in turn, infected the females. One female was fatally infected with the fungus without contact with a field-caught male, presumably as a result of carry-over of spores in the soil medium.

The mean total of eggs laid by 31 productive females was 30 ± 7 (95% c.l. from normal distribution), with a range of 8 to 76, but some females died without ovipositing.

Longevity of adults.—The mean preoviposition period for 30 *S.a. grossepunctatus* females was 69 ± 6 d (95% c.l. from normal distribution). The mean oviposition period of 29 insects was 48 ± 7 d (95% c.l. from t since $n < 30$). The mean total adult life span of 30 females was 115 ± 6 d (95% c.l. from normal distribution). The mean adult life of 25 males was 116 ± 9 d (95% c.l. from t since $n < 30$).

Natural enemies

Predators, parasites and diseases seemed to be of little importance in the field.

Predators.—The introduced assassin bug *Platymeris laevicollis* Distant is predacious on *O. monoceros* adults in palm crowns in Kenya, and on caged *O. rhinoceros* adults in the insectary, but although it has been released at several sites in New Ireland and New Britain, there is no evidence of its establishment. A captive specimen of the nocturnal marsupial flying phalanger (*Petaurus breviceps papuanus* Thomas) which lives in the tops of some dead standing palms, readily attacked and ate dynastid adults, consuming about one adult per night. Elaterid larvae, known as predators of *Oryctes* larvae elsewhere (Catley 1969), were rarely found in breeding places in New Guinea. In general, the impact of predators on field populations of these beetles and their larvae, which are largely cryptic, is difficult to assess.

Parasites.—Releases of the wasp *Scolia ruficornis* F. (introduced from Zanzibar) were made at Vunapope, Gazelle Peninsula in the early 1960's (Dun, undated), but sampling by the author of large numbers of *O. rhinoceros* larvae from this area during 1968 to 1971 failed to reveal any parasitism by this or any native scoliids. Nor were any tachinid parasites of the adults observed. Six of 21 *O. rhinoceros* larvae collected from plantations in the Gazelle Peninsula in March 1968 had one or more oxyurid nematodes in the fermentation chamber of the gut, but it is doubtful if they harm the larvae (Bedford 1968).

Rhabditid nematodes have been reported from the aedeagus, the bursa copulatrix and the colleterial glands of *O. monoceros* in Kenya (Hoyt and Catley 1967) and the Ivory Coast (Poinar 1970, 1971), various *Oryctes* species in Madagascar (Bedford 1968) and *O. centaurus* in New Guinea (Hoyt and Catley 1967). Hoyt (undated) also found nematodes in the colleterial glands of the dynastines *S.a. australis*, *S.a. grossepunctatus*, *Oryctoderus latitarsis Boisduval*, *O. rhinoceros* and *Xylotrupes gideon ulysses* Guérin, but not in the aedeagus or bursa copulatrix of these species.

The following adult dynastines from New Guinea have now been examined for nematodes: *O. rhinoceros* (66 ♂, 109 ♀), *S. australis* (72 ♂, 37 ♀), *X.g. ulysses* (8 ♂, 34 ♀), and *Oryctoderus* sp. (8 ♂, 8 ♀). Nematodes were detected in the aedeagi of 56% of *S. australis* males (*c.f.* Hoyt, undated), in 8% of *O. rhinoceros*, in 75% of *X.g. ulysses* and 25% of *Oryctoderus* sp. Examination of the colleterial glands of females revealed nematodes in 26 of 28 *S. australis*, 20 of 68 *O. rhinoceros*, 26 of 27 *X.g. ulysses* and 75% of *Oryctoderus* sp. Nematodes were absent from the bursa copulatrix of all *O. rhinoceros* and *Oryctoderus* examined but were present in one instance in *S. australis* and doubtfully in one *X.g. ulysses*. This contrasts with *Oryctes* spp. in Madagascar and Africa where nematodes are abundant in the bursa.

Gregarine cysts were often detected under the terminal abdominal integument of *S.a. grossepunctatus* L3 reared in the insectary, but these appeared to be without harmful effect, and infected larvae developed and pupated normally. A similar conclusion was reached by Hüger (1968) who studied the gregarine *Stictospora kurdistana* Theod. from *Oryctes* sp. larvae collected by Bedford (1968) in Madagascar. In insectary-reared *S.a. grossepunctatus* adults, 6 of 12 males dissected contained 2 to 15 cysts, and four of 17 females contained 4 to 6 cysts. These infections were presumably derived from the soil oviposition medium in which the adults were kept.

Field infestation of *Scapanes* appeared to be of a low order, for of 130 wild-collected adults dissected, only 4 contained gregarine cysts.

Diseases.—The fungus *M. anisopliae* infected a small percentage of *O. rhinoceros* larvae in the field in Western Samoa (Maddison and Zelazny 1970), Malaysia (Surany 1960) and Madagascar (Bedford 1968), as well as laboratory cultures in France (Hurpin and Fresneau 1967). However, 596 *O. rhinoceros* L3 collected by the author in the Gazelle Peninsula and New Ireland, and held in individual tins in the insectary, showed no sign of such infection, nor was the fungus observed on larvae or adults in the field. A small number of reared larvae developed the infection in the insectary. A small proportion of *S.a. grossepunctatus* were infected by *M. anisopliae* in the field. A sample of 1169 adults from a large plantation at Kabaira, Gazelle Peninsula, collected between 20.x.70 and 21.i.71 and held in the insectary showed a mortality of 2.4% due to this cause, but only one of 177 larvae reared *ab ovis* did so.

Competitors for breeding sites.—A variety of arthropods inhabit decaying wood and, if they occur in large numbers, they may directly compete with dynastid larvae for the wood as food or, alternatively, their presence may accelerate the breakdown of the wood, thus limiting that available to dynastines. Coleoptera and Diplopoda were most frequently encountered in New Guinea and the Solomon Islands.

The ecology of Passalidae is probably typified by that of *Passalus cornutus* F., studied by Pearse et al (1936) in North America. In New Guinea, passalids such as *Labienus ptox* (Kaup) frequently occurred in decaying logs in forests, and in decaying palm logs on the ground, and they appeared to have a significant effect in breaking down the coconut wood. At Yandina in the Solomons, *Protomocoelus australis* Boisduval was associated with millipedes in coconut logs, which the passalids appeared to prefer to other types of decaying wood, even though coconut wood was not as abundant. Passalids were seldom observed in the tops of dead standing coconut palms, but in one instance, a group of three dead standing palms at Kabaira Plantation, New Britain, showed numerous larvae and adults of a small passalid, in addition to abundant *O. rhinoceros* larvae. Passalids and *O. rhinoceros* larvae occasionally occur together in decaying coconut trunks on the ground.

Millipedes were commonly encountered in decaying logs. In particular at Yandina, in July 1969 *Acladocricus* sp. was very active, in association with passalids, in breaking down decaying coconut trunks. The palms in question were 8 to 9 years old, but many had been felled by the cyclone of March 1967. Millipedes were also found in decaying trunks other than coconut at various sites in New Guinea.

Lucanid and cetoniine larvae were widely distributed and fairly commonly found in decaying trunks, but their numbers in any particular site were probably too low to have a marked effect in breaking down the trunks. Cerambycid larvae were frequently found in coconut logs on Efate Is. in the New Hebrides, but in New Guinea were seldom observed in such sites.

Discussion

The present work has shown that there are important differences in the biology and ecology of *O. rhinoceros* and *S. australis*, and that there is little competition between them. *O. rhinoceros* is very versatile in that it can use a wide variety of breeding sites. In coconut growing areas, decaying palm wood is important either in the form of dead standing poles (e.g. tall palms killed by lightning strike or shorter palms killed by *Rhynchophorus* weevil attack), coconut trunks on the ground, or stumps. Thus plantation hygiene is very important in *O. rhinoceros* infested areas. *S. australis* larvae, on the other hand, were never found associated with decaying coconut wood but only under decaying trunks of bush trees, and in areas where only this species occurs, the removal of palm logs and stumps is not essential. Coconut trunks may safely be left to decompose *in situ*, with considerable savings in cost and labour. But where forest or other types of trees are being cleared to prepare land for the planting of coconut, the trunks and stumps should preferably be burned, broken up, or at least covered with a leguminous cover crop, such as *Pueraria*.

S. australis differs from *O. rhinoceros* in its sparse larval distribution at breeding sites, and the two species diverge widely in the length of their life cycles, and in their preferences for young and mature palms, respectively. Thus the appearance of damage in hitherto unaffected stands of tall palms may be taken as evidence of the recent arrival of *O. rhinoceros* in the area. In the field one species does not exclude the other or prevent it from becoming established and, in fact, they co-exist in the Gazelle Peninsula of New Britain and New Ireland. The activities of both species can also facilitate infestations of the palm weevil *Rhynchophorus bilineatus* Montrouzier which frequently oviposits in their workings. This weevil can be a serious pest of palms in the Gazelle Peninsula (Smee 1965), but did not seem important in the Solomon Islands.

Since predators and parasites are evidently of limited effect in restricting the size of the rhinoceros beetle populations in New Guinea, the main factor appears to be the number of suitable breeding sites. Indeed, it is frequently observed that where adequate numbers of breeding sites occur in a localised situation, large beetle populations can soon build up, while remaining low in areas with few breeding sites. This accounts for the wide variation in levels of palm damage from one site to another.

The *Scapanes* problem, although sometimes serious, is a transient one in any given new plantation, for once the debris resulting from bush clearance has rotted away or become concealed adequately by ground cover, this species permanently declines. Moreover, palms in the susceptible age group are easily reached and may be protected by periodic applications of 1:9 mixture of 6.5% gamma BHC and sawdust (Catley 1969), or of lindane granules, to the axils of the fronds.

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