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New aspects of the biology of the Melanesian rhinoceros beetle *Scapanes australis* (Col., Dynastidae) and evidence for field attraction to males

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Abstract: *Scapanes australis* is a major coconut pest, endemic in Papua New Guinea. Early in the night, males placed singly into artificial galleries made in young coconut palms exhibited a sex-specific calling behaviour for 1 to 1.5 h. Coming to the gallery entrance, they raised the abdomen and the hind legs, the head lowered inside the gallery, and emitted a liquid secretion, rhythmically smeared by crossing the legs. Females, which did not behave so, were very mobile. The adult flying period coincided with the male calling behaviour. In field assays with caged insects on coconut palms, attraction of both sexes to males was evidenced when they were calling. Males fought for gallery possession at a male arrival. No aggression but mating was observed with arriving females, which proved not to have developed oocytes. The strong male attraction was confirmed using automatic traps, baited with one live male in a sugarcane piece. Males were assumed to release an aggregation pheromone. Further studies are underway to identify the putative pheromone.

1 Introduction

Scapanes australis Bsdv. (Col., Scarabaeoidea, Dynastidae), further referred to as *Scapanes*, is a 4 to 6 cm long beetle and a major coconut pest endemic in Papua New Guinea, the Solomon Islands and Indonesia (Irian Jaya). Five subspecies have been described, three from Papua New Guinea Mainland, one from the Bismark Archipelago, and one from the Solomon Islands (BEDFORD, 1976; DECHAMBRE, 1995). All subspecies attack coconut as well as native palms and occasionally unrelated plants such as banana trees.

The adults are good nocturnal flyers. They mine galleries in the bases of fronds where they hide during daytime. The galleries frequently destroy the growth point in young coconut palms (CPs). In spite of low populations (< 5 insects/ha; BEDFORD, 1975) but given the beetle size and mobility, serious damage is caused to the palms. *Scapanes* damage attract Black Palm Weevils (BPWs), *Rhynchophorus bilineatus* (Montr.), which lay eggs. The weevil larvae cause new damage. The combined *Scapanes*–BPW attacks are very common and lead inevitably to the death of the CPs.

Insecticide control of *Scapanes* is only effective if applications are often repeated, which has become incompatible with safeguarding the environment (SMITH, 1981). Smallholders cannot afford to use insecticides because of cost. Moreover it is very difficult to collect the adults and extracting them from the galleries causes more damage.

Extensive studies on the biology of *Scapanes* have been undertaken over the past 25 years to develop new control methods but without success (HEARD, 1972; BEDFORD, 1975, 1976; MACFARLANE, 1983; WATERHOUSE and NORRIS, 1987; MOXON and HELA, 1989). This failure has presently led to the abandonment of programmes of coconut development in the East New Britain province of Papua New Guinea.

A prospective way of reducing *Scapanes* damage is to eliminate the adults by selective trapping using attractants. Great hopes have been placed in this system as pheromones have been recently identified in the Dynastidae *Oryctes monoceros* (Oliv.) and *Oryctes rhinoceros* (L.) (GRIES et al., 1994; HALLET et al., 1995; MORIN et al., 1996). In the latter species, trapping adults with synthetic pheromone is being developed in Indonesia and Malaysia as an efficient tool for pest management (HO, 1996).

Past studies on *Scapanes* biology pointed out that many more males than females were captured on CPs (male : female, 3.9 to 6.5 : 1; HEARD, 1972; BEDFORD, 1975). Single *Scapanes* were generally males. Groups of beetles were rare and most frequently mixed. The sexes behave very differently: The male could stay in the palm for several weeks whereas the females visited the palm for only 1 or 2 days (MACFARLANE, 1983). Opposite conclusions about a sex attraction have been made: the female could be attractive according BEDFORD (1975), the male according to MOXON and HELA (1989).

We report here new data documenting the existence of a peculiar male calling behaviour and evidencing the field attraction of conspecifics to calling males at night.

2 Materials and methods

The work was carried out on *Scapanes australis grossepunctatus* Stern. at Keravat CCRI Station (East New Britain

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province) and on *Scapanes australis australis* at Murnas CCRI Research Station and on Karkar Island (Madang province).

2.1 Analysis of natural distribution of *S. australis* on CPs

Scapanes adults were collected during two periods from a 35 ha planted area: January–June 1997 and November 1997 (routine survey in CCRI coconut plots). The number and sex of the beetles collected in each CP attacked were recorded. The shape of the gallery (simple or branched) and the position of the beetles within the galleries were recorded in the Nov 1997 survey. The CPs were 1.5 to 3 m tall. From January–June 1997 data, the relationship between sex-ratio and *Scapanes* density in each damaged CP was tested by analysis of variance (ANOVA), using a generalized linear model (GLM) with logit male proportions as the response variable and density as a factor (levels: 1, 2, 3 or 4). The analyses were weighted for sample size assuming the errors in the response variable followed a binomial distribution. A step-wise process of model simplification was used to determine the 'minimal adequate model', where all parameters significantly differed from zero and from one another ($\alpha = 0.05$). The process began with the full model, then grouped together adjacent factor levels that did not differ from one another (CRAWLEY, 1993). Analyses were made using S-PLUS statistical software (STATISTICAL SCIENCES, 1993).

2.2 Preliminary adult manipulation and artificial settlement for behaviour studies and experimental field trapping

Field-collected males or females were placed into artificial galleries (diameter = 3–4 cm; L = 5–6 cm) prepared either in field-planted (5- to 8-year-old) or in nursery (12- to 18-month-old) CPs at the base of a frond axil. For the trapping assays, a wire cage was added to prevent beetles from escaping. The assay consisted of preparing and observing batches of 4–12 insects of each sex according to *Scapanes* availability. Beetles were placed singly in artificial galleries mostly at 1500h. The behaviour of 50 males and 35 females was recorded from 1800 to 2030 h (dusk on 1815 h $\pm$ 0015). Each insect was observed every night until it escaped. Observations were made over 6 months in 1997: assay 1, field planted CPs with only males placed in artificial galleries; assay 2, nursery CPs installed in the laboratory; and assay 3A, nursery CPs + cages in the field, with males and females.

In assays 1 and 2, qualitative observations were made to describe the general pattern of insect activity in connection with the time in the day. In the field (assay 1 and 3A), *Scapanes* arrivals to the beetles artificially settled were recorded and qualitative observations were made to describe the behaviour of the arriving and of the settled beetles, according to sex. The proportion of caged *Scapanes* performing the various behaviours described were quantified in assay 3A. Activity patterns between males and females were compared using χ^2 tests on the contingency tables.

2.3 Experiments to evidence field attraction to live *S. australis* and/or CPs

2.3.1 Assay 3A (Keravat; 19 November to 2 December 1997)

To avoid damaging planted CPs and set up the assay at a site under controlled conditions, we used 18-month-old nursery CPs with an artificial gallery prepared as described previously. The gallery entrance was covered with a wire (1 cm square mesh) guard (12 cm × 12 cm × 12 cm) to prevent the live *Scapanes* bait from escaping. The CPs prepared in this manner (experimental) are further referred to as XCPs. The bait insects were collected the day before from coconut plots. The XCPs were taken to a cleaned plot planted with 6-month-old cocoa trees provided with shading by *Gliricidia sepium* (Jacq.) trees. The XCPs were positioned approximately 6 m apart along four windrows and attached to the trunks of *G. sepium*.

The assay consisted of three treatments, each replicated eight times: (a) an XCP + one male; (b) an XCP + one female; (c) an XCP without insect. The XCPs were positioned in two complete groups of treatments along each windrow with random positioning of the treatments within each group. The XCPs were kept at the same place all along the assay to avoid insect disturbance. The cages fitted to the XCPs were observed daily from 1800 to 2000 h. Additional checks were made once later in the night at 2100, 2300 and 0430 h.

The beetles which arrived on, or near (< 0.5 m), the XCPs were immediately collected and isolated. The sex-ratio of the cumulative catches from each treatments were compared using a χ^2 test on the contingency table. Mean catches per treatment were compared by a Kruskal–Wallis test ($\alpha = 0.05$). The times of arrival were recorded.

Females were dissected the day after to examine the organization of their reproductive organs (fig. 1). Sixteen females (out of 20) attracted in assay 3A were dissected to determine their reproductive status. Seven females from natural galleries were studied for comparison. Ovary development (no. of oocytes and eggs within four size classes; see table 3) and the state of the bursa copulatrix (presence of spermatophore and spermatozoids) were examined.

2.3.2 Assay 3B (Keravat; 2–19 December 1997)

The assay was set up using three groups of six XCPs prepared as in assay 3A. The XCPs, spaced 5 m apart within each group, were installed at three sites. The sites were 50 m apart along a line (control XCPs between the insect-baited ones) and located in a 15-year-old cocoa–coconut plot. Observations have been carried out every evening for 2 weeks. The groups of XCPs with caged males and females were switched the second week. All XCPs and dead insects were then replaced. Mean catches per treatment (cumulative for 1 week and the six XCPs) were compared by ANOVA on $\ln(x + 1)$ transformed data followed by Newman–Keuls test with $\alpha = 0.01$.

2.3.3 Assay 3C (Keravat; 2–16 January 1998)

A simplified design (eight replicates) was set up to compare the effect of *Scapanes* male + plant to the sole plant (control). A piece of sugarcane, instead of CP, was used to settle the male. An automatic trap was developed at the same time (KAKUL et al., 1998) by modifying the BPW bucket trap from OEHLSCHLAGER et al. (1995). A cage containing the plant piece with or without one male was fixed below the trap lid. The bucket was modified with a simple internal barrier which enabled lured beetles to enter but not to escape. No pesticide was used. Traps were disposed along two 150 m distant rows of CPs. The traps were separated by 50 m along each row and treatments alternated. Catches were recorded daily over a period of 14 days. Mean catches per treatment were compared by Student's *t*-test.

2.3.4 Assay 4 (Tavilo; 4 April to 18 May 1998): Development of a routine trapping with live S. australis *male as bait*

The positive results of assays 3A–3C and the urgency to improve *Scapanes* control in plots of CPs prompted development of the use of the live male-baited traps. Twenty automatic male-baited traps were installed on a 2 ha plot in Tavilo

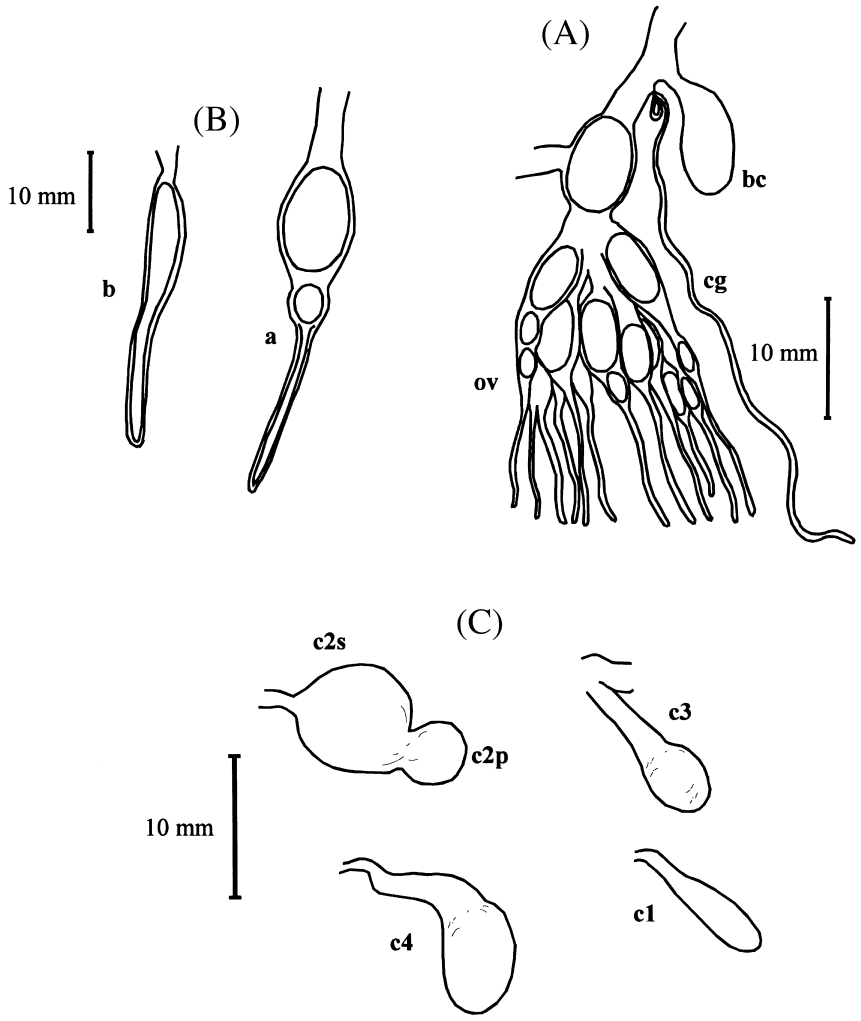

Fig. 1. *Female reproductive organs of* Scapanes australis grossepunctatus. *(A) One ovary with 12 ovarioles (ov), colleterial gland (cg) and bursa copulatrix (bc). (B) Ovarioles (a) young ovariole with oocyte in maturation (b) young ovariole without oocyte of immature female. (C) Shape of various bursa copulatrix: (c1) empty bursa (c2) just after mating with (c2s) a large spermatophore and (c2p) the remainder of an old spermatophore (pasty material) (c3 and c4) with remainders of an old spermatophore (pasty material)*

CCRI research Station on a 30 m × 30 m grid. The treatments were randomly distributed. Traps were checked, dead male-bait changed and sugarcane renewed weekly. The balance of the capture sex-ratio was tested by Wilcoxon's paired-test on numbers of males and females. The sex-ratio of the catches obtained from natural CP galleries (January–June 1997 survey) by day and of the beetles trapped in assay 4 were compared using a χ^2 test on the contingency table.

3 Results

3.1 Distribution of naturally settled *S. australis* in damaged CPs

A total of 108 males and 41 females were collected over 5 month survey from 106 damaged CPs (January–June 1997; table 1). Thirty-two were collected over the fortnight survey in November 1997 from 22 damaged CPs. In 55 and 68% of cases (January–June and November 1997, respectively) a single *Scapanes* was found in the galleries. Group size did not exceed four individuals and the sex-ratio was highly in favour of the males (3.0 : 1 and 4.3 : 1, respectively). The GLM analysis indicated that the sex-ratio of the insects found singly on the CPs is significantly different from that of the insects in groups ($\chi^2 = 7.07$; 1 d.f.; $P < 0.008$). Single insects are mostly males, whereas groups are basically mixed. The six groups of *Scapanes* observed in Nov. 97 revealed that the *Scapanes* in contact in a gallery were all male–female pairs. When two males were found on the same CP, they were separated by at least 10 cm, each one being in each arm of a branched gallery with a common entrance or at the two extremities of an unbranched gallery.

3.2 Qualitative behavioural patterns of *S. australis* placed in artificial galleries

Both sex *Scapanes* excavated immediately once placed and went on tunnelling the artificial gallery in approximately two-thirds of cases. A placement at 1500 h was optimal to obtain maximum settlement. On the first night after placement, both males and females were most often found inside the galleries with signs of feeding and excavating – a pile of freshly chewed stem tissue at the gallery entrance.

From the second or the third night, the following behavioural pattern was recorded from males only. Soon after nightfall, the male moved to the entrance and took up a peculiar position: the abdomen emerged from the gallery although the head and prothorax remained inside the gallery, in general hidden in chewed plant tissues. The body was maintained more or less perpendicular to the plant axis, almost motionless with

Table 1. *Distribution of* Scapanes *collected during the day in naturally infested coconut palms: Keravat, Papua New Guinea; January–June 1997*

Density per coconut palm	Sexes		No. records	Total no. *Scapanes*		
	Male	Female		Male	Female	Total
1	0	51	51	51	*	
	0	1	8	*	8	
	Total		59	51	8	59
	Sex-ratio			6.4	: 1	a
2	2	0	14	28	*	
	1	1	24	24	24	
	0	2	0	*	0	
	Total		38	52	24	76
	Sex-ratio			2.2	: 1	b
3	3	0	3	9	*	
	2	1	3	6	3	
	1	2	2	2	4	
	0	3	0	*	0	
	Total		8	17	7	24
	Sex-ratio			2.4	: 1	b
4	4	0	0	0	*	
	3	1	0	0	0	
	2	2	1	2	2	
	1	3	0	0	0	
	0	4	0	*	0	
	Total	1	2	2	4	
	Sex-ratio			1.0	: 1	b
All densities			106	122	41	163
	Sex-ratio			3.0	: 1	

*indicates that no catch is possible.
Sex-ratios followed by the same letter are not different (ANOVA on GLM model; $\alpha = 0.05$; see text for detail).

the hind legs raised in the air. The pygidium slightly half-opened every 20 to 30 s. It released a droplet of liquid in most cases, which the insect smeared onto the ventral part of its pygidium with the hind tarsi by a rhythmic crossing of its legs. The whole behavioural sequence will be subsequently referred to as 'performing'(fig. 2).

In Papua New Guinea, 75–90% observed males were 'performing' at night. When occurring, this peculiar behaviour has been observed for 1–1.5 h, rarely for a shorter or a longer period. 'Performing' males were highly sensitive to plant-borne vibrations caused by touching, even lightly, the fibres at the gallery entrance or a coconut frond, even 3 to 4 m distant from the gallery (assays 1–3A). They systematically stopped 'performing' and rapidly withdrew into the gallery as soon as they perceived vibrations. The withdrawal was short-lived only if the disturbance was slight and occurred at the start of the 'performing' period. The secretion released by 'performing' males was whitish or limpid with a characteristic odour. The amount released was very variable from one male to another, whatever the location and conditions. The emission of secretion by a given male varied from one day to another. Females never behaved as described under 'performing'. They usually remained for only one night in the galleries and were highly mobile in or around the gallery all through the night once artificially placed (assays 2–3A). Females were observed to occasionally emit liquid from the pygidium, which clearly differed in its odour from male secretion.

3.3 Qualitative behaviour of arriving *Scapanes* to artificially settled *Scapanes*

3.3.1 Observations of flights and landings

While observing artificially settled males in assay 1, *Scapanes* were heard flying at nightfall. *Scapanes* is a clumsy flier. Nine males and 12 females landed near the galleries containing one 'performing' male and were caught between 1830 and 1900 h. These observations were confirmed in assay 3A (Section 3.4.2; fig. 3). The approaches of males and females to the caged males were similar (10 observations). Some insects flew straight in and landed directly on the cages. Other ones landed on a leaf 10–20 cm away from, and then walked to the cage.

3.3.2 Male aggression towards other males

Arrival of a male *Scapanes* to a 'performing' male always resulted in a confrontation (nine cases). Contact between the two males elicited a sharp audible hissing sound and the arriving male tried to pull the resident male out of the gallery. The frontal horn, if well developed, was used to hook out the resident on some occasions. Invariably the larger specimen gained or remained in possession of the gallery. Fights could last 10–20 min.

3.3.3 Male behaviour towards a female and mating

After the arrival of a female to a 'performing' male (12 cases) the contacts with the tarsi were usually followed

Fig. 2. *Male* Scapanes *'performing' at the entrance of a gallery in a nursery coconut palm installed in the laboratory (Keravat, CCRI research station, Papua New Guinea). The peculiar behaviour (abdomen and hind legs raised; pygidium emitting a liquid secretion) was observed at the beginning of the night and corresponds to a calling behaviour*

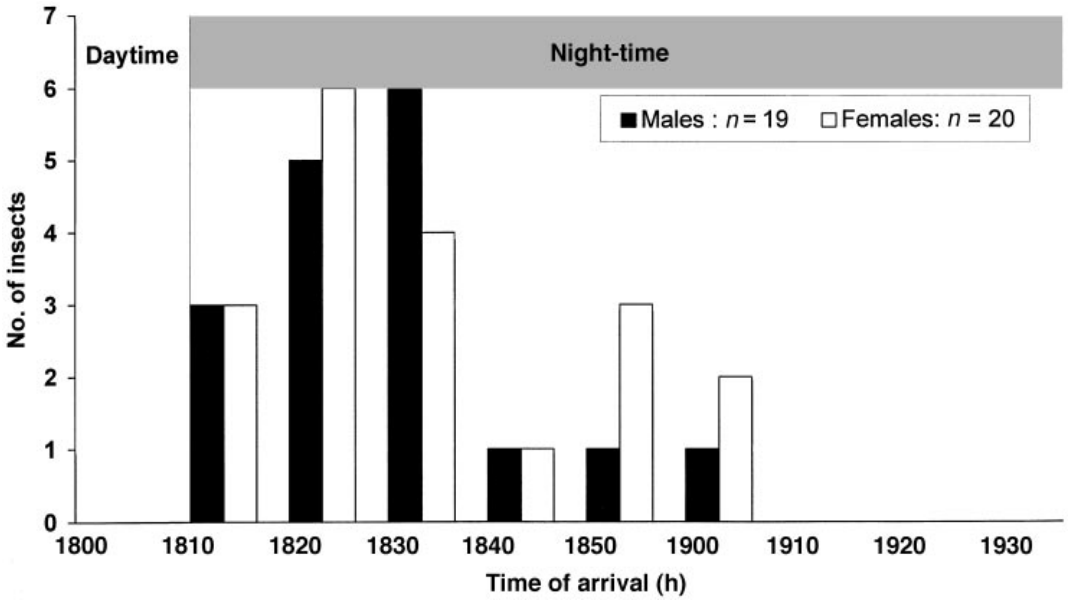

Fig. 3. *Times of* Scapanes *arrival to experimental (*Scapanes*-baited) coconut palms in assay 3A; Keravat, Papua New Guinea; 19 November – 2 December 1997*

by the releasing of strong sounds by both insects. No aggressive behaviour was observed from the male. In most cases, the female entered the gallery, the male followed her and mating occurred near or in the entrance. The male sometimes left the gallery and mating was observed to take place immediately outside, adjacent to the entrance. Observed pairing lasted up to 1 h. The male generally followed the female deep inside the gallery after partner separation. From observed mating cases, the females usually only stayed one or two nights before leaving the male. These males could attract other *Scapanes*, and some have been recorded as staying in the same gallery for 2 weeks.

3.4 Quantitative description of the behaviour of *S. australis* placed in artificial galleries (assay 3A)

3.4.1 Behaviour of caged insects

Night fell between 1800 and 1815 h. Most insects were in their galleries and a few were immobile at the entrance at 1800 h. Just after passing to darkness, the males took

Table 2. *Comparative behavioural patterns of caged male and female* Scapanes *in assay 3A in the evening between 1815 and 1900 h and later at night; Keravat, Papua New Guinea; 19–28 November 1997*

		Scapanes behaviour on coconut palm ($n = 8$)				
			at entrance			
Dates and times	Sex	inside gallery	immobile	'performing'	moving outside	χ^2 (d.f.) male vs. female
18–25 Nov. 1815–1900 h	Male	0.0 ± 0.0	0.5 ± 0.8	7.5 ± 0.8	0.0 ± 0.0	16.0 (3)
(m ± SD)	Female	2.5 ± 2.4	0.5 ± 0.8	0.0 ± 0.0	5.0 ± 2.6	***
Other times						
22 Nov 2130 h	Male	8	0	0	0	0.6 (1)
	Female	6	0	0	2	NS
22 Nov 2330 h	Male	6	2	0	0	0.3 (1)
	Female	4	4	0	0	NS
23 Nov 0430 h	Male	6	2	0	0	6.0 (2)
	Female	2	2	0	4	*

An average of the 8 days of observation is presented for the evening records.
'Performing': behaviour, see text for detail.
The differences (χ^2 tests) between male and female behavioural patterns are: NS, not significant, $P > 0.05$; significant: *, $P < 0.05$ and ***, $P < 0.001$.

up their 'performing' position while most females came out and moved around in the cages. Four behaviour patterns were observed: 'performing', only by males; moving outside the gallery in the cages, only by females; hidden inside the galleries; and immobile at gallery entrances. The behavioural patterns from males and females were significantly different ($\chi^2 = 16.0$; 3 d.f.; $P < 0.001$) in the first hour of the night (1815–1915 h). These patterns were similar from one day to another. The males progressively stopped 'performing' during the second hour of the night. They went back into their galleries, without returning, at around 2000 h. The three visits in the middle of the night showed that males were nor outside the galleries nor 'performing'. Most insects were inside the galleries with few if no difference between male and female behavioural patterns at that time. The females were sometimes still active (table 2).

3.4.2 Scapanes *arrivals*

They arrived between 1815 and 1915 h (fig. 3; assay 3A). Maximum arrivals occurred between 1820 and 1840 h for both sexes. More females than males arrived in the latter part of the flying period. During the extra night-time visits, no *Scapanes* were seen or heard. In assay 3B, the beetles arrived at the same time: 21 insects (91%) arrived between 1820 and 1910 h and two females were caught at 1930 h.

3.5 Catches at *Scapanes*-baited XCPs and *Scapanes* attraction to conspecifics

3.5.1 Comparative assays 3A–C

Assay 3A: Thirty-nine insects (19 male, 20 female) were collected from the XCPs (fig. 4). The sex-ratio of the arrivals was balanced considering both the total catches and the distribution between the treatments ($\chi^2 = 1.35$; 2 d.f.; $P = 0.5$) About four times more *Scapanes* arrived to the male-baited than to the female-baited or the insect-free XCPs. This difference was not significant ($H = 3.18$; 2 d.f.; $P = 0.2$) due to substantial heterogeneity in the replicates.

Assay 3B: Twenty-three beetles (seven male, 16 female) arrived at XCPs with males and none at the XCPs with females or without insects. The male effect was highly significant ($F_{2,3} = 74.62$; $P < 0.003$).

Assay 3C: Twelve beetles (six male, six female) arrived at XCPs with males and none at the insect-free control. The male effect was highly significant ($t = 3.55$; 7 d.f.; $P < 0.005$; one-tailed test). No dead male bait were recorded during the assay.

3.5.2 Reproductive state of females collected in assay 3A

Preliminary dissections showed that the females possessed two pairs of 12 ovarioles, a common oviduct with a collateral gland and a large bursa copulatrix (fig. 1). Different physiological states were characterized by examining the bursa copulatrix and ovary developments (table 3):

(i) Immature virgin female: flat, empty bursa copulatrix; poorly developed ovaries with ovarioles containing no visible oocytes or only small-to medium-sized forming oocytes.
(ii) Just mated female: bursa copulatrix swollen by a large whitish spermatophore plus an orange-coloured pasty substance from old spermatophores; developed ovaries with ovarioles containing small- and medium-sized maturing oocytes.
(iii) Formerly mated female: bursa copulatrix with or without living visible spermatozoids, but slightly swollen and with the orange-coloured pasty substance described above; developed ovaries with ovarioles containing large-sized oocytes with or without completely developed eggs (approximately 3 mm).

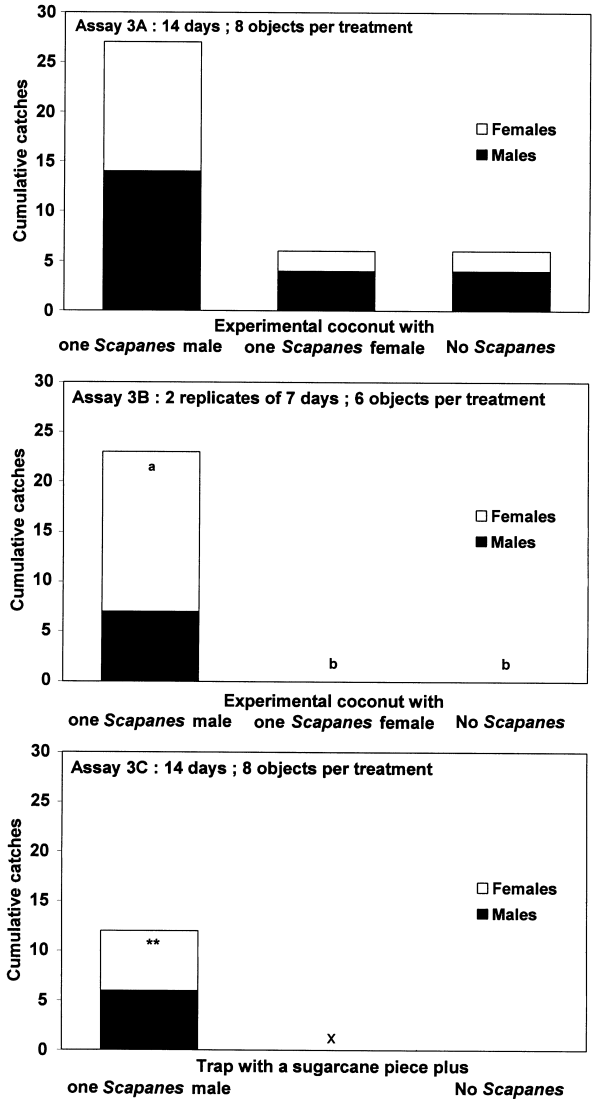

Fig. 4. *Total* Scapanes *captures with caged conspecifics placed on coconut palms or in sugarcane at Keravat, Papua New Guinea (assays 3A: 19 November – 2 December, 3B: 2–19 December 1997 and 3C: 2–18 January 1998). The experimental object was: one nursery coconut with or without one* Scapanes *(assays 3 A–B) or one sugarcane-baited trap with or without one male* Scapanes *(assay 3C). Assay 3A: objects spaced by 6 m along four rows and semi-randomly distributed. Treatments are not significantly different (Kruskall–Wallis H-test on mean-ranked total catches during 14 days; 2 d.f.; $P = 0.2$). Assay 3B: objects grouped (5 m spacing) by treatment. Groups spaced by 50 m. Treatments associated to the same letter are not significantly different ($\alpha = 0.01$; Newman–Keuls test on mean total weekly catches per group after $\ln(x + 1)$ transformation). Assay 3C: traps spaced by 50 m and disposed along two 150 m distant rows. Treatments alternated. × , no 'one female treatment' in this assay; **, treatments are significantly different (Student's* t*-test on mean total catches per trap during 14 days; $P < 0.005$)*

Nineteen out of 23 females had already mated when they were dissected wherever they were collected. None of the 16 females attracted to the XCPs in assay 3A had eggs ready to be laid nor possessed many large-sized oocytes (table 3). On the contrary, the seven females collected by daytime from natural galleries or around houses, had significantly more eggs and more large-sized oocytes ($t = 2.29$, 6 d.f., $P < 0.03$ and $t = 2.88$; 7 d.f., $P < 0.01$, respectively). Such differences existed relative to the sole females captured at male-baited XCPs ($t = 2.29$; 6 d.f.; $P < 0.03$ and $t = 2.82$; 7 d.f.; $P < 0.01$, respectively). Females of both origins possessed nonsignificantly different numbers of medium- and small-sized oocytes.

3.5.3 Larger-scale catches in traps baited with live male S. australis *(assay 4)*

Assay 4 demonstrated that the attraction to male *Scapanes* was a consistent and intense phenomenon (table 4). An efficient trapping strategy could be developed using live male-baited traps with plant pieces. Sugarcane was a suitable substitute for coconut for *Scapanes* settlement and further conspecific attraction to the bait. The captures using this new trapping system (191 beetles) were higher in 1.5 month (2 ha) than in 6 months (January–June 1997) by checking natural galleries in CPs (163 beetles) over 35 ha. The sex-ratio of the trapped beetles was significantly unbalanced towards females (0.5 : 1, male : female; Wilcoxon's paired-test; $W = 0$; 6 d.f.; $P < 0.01$). It was significantly different from that of the beetles from natural galleries in January–June 1997 (3.0 : 1; $\chi^2 = 60.87$; 1 d.f.; $P < 0.001$).

4 Discussion

Male *Scapanes* were much more abundant than female in the CP galleries by daytime as reported by BEDFORD (1975) and by HEARD (1972) whereas the sex-ratio of emergent adults was balanced (BEDFORD, 1975). The galleries contained mainly a single insect and no groups larger than four individuals were found. The distribution and the sex-ratio of the so collected *Scapanes* were not hazardous: single beetles were more often males and groups were more often mixed. PRIOR (unpublished results) never observed females naturally initiating galleries contrarily to males. These data supported the hypothesis of a primary selection and attack on the CPs by the males with a subsequent arrival of females. The presence of females mostly with males suggested the 'male-damaged CP' complex to trigger female orientation towards the CPs.

Males obviously avoided each other when they were found on the same CP (branched or separated galleries). The repeated observations of male fights provided an explanation for this. The male had a territorial behaviour once settled on a CP and did not accept the presence of a competitor in a gallery that it occupied. This ecological feature is common in the Dynastidae and Lucanidae families; fights occur either to gain possession of a suitable host plant or a mate (EBERHARD, 1979, 1980). In *O. rhinoceros*, another species economically damaging palms, such behaviour has not been reported yet and, on the contrary, the adults tolerate promiscuity in compost.

Table 3. *Quantitative description of the reproductive apparatus of* Scapanes *females collected in various situations (Keravat, Papua New Guinea; November 1997)*

Female origin		Bursa copulatrix		Ovaries (mean ± SD no. of cells/insect)			
					oocytes		
		empty: virgin	+ pasty material (sperm.): mated	eggs	large	medium	small
Assay 3A at experimental coconut palms	with caged males ($n = 10$)	2	8 (2)	0.0* ± 0.0	1.0* ± 1.4	8.7 ± 5.2	17.6 ± 5.8
	with caged females ($n = 4$)	1	3 (2)	0.0 ± 0.0	1.0 ± 1.2	9.5 ± 3.4	22.5 ± 5.8
	without insect ($n = 2$)	0	2 (0)	0.0 ± 0.0	1.0 ± 1.4	1.0 ± 1.4	13.5 ± 6.4
	Total	3	13 (4)	0.0* ± 0.0	1.0* ± 1.3	7.9 ± 5.1	18.3 ± 6.1
Other	at light around houses ($n = 3$)	1	2 (0)	8.0 ± 8.0	6.0 ± 5.2	5.0 ± 5.0	6.7 ± 7.0
	in natural palm galleries ($n = 4$)	0	4 (1)	3.3 ± 4.3	5.3 ± 3.9	8.5 ± 1.7	20.5 ± 13.1
	Total	1	6 (1)	5.3* ± 6.1	5.6* ± 4.1	7.0 ± 3.7	14.6 ± 12.5

Large oocytes: 2–3 mm; medium oocytes: 1–2 mm; small oocytes: 0.3–1 mm; eggs: > 3 mm, free when ovaries dissected. Oocytes < 0.3 mm were not counted.
SD, standard error of the mean.
Sperm, with living spermatozoids.
*, significant ($\alpha = 0.05$) difference with females collected in assay 3A, either with only caged males or with all treatments (Student's *t*-test).

Table 4. *Captures of* Scapanes *in male* Scapanes*-baited traps in assay 4 (Tavilo, Papua New Guinea; 4 April – 18 May 1998) compared with captures in natural galleries on coconut (Keravat, Papua New Guinea; January–June 1997)*

Capture origin	Week	Male	Female	Total
Assay 4: Automatic male-baited trap + sugarcane piece (1.6 month; 2 ha; 20 traps)	1	12	31	43
	2	11	12	23
	3	16	22	38
	4	8	16	24
	5	8	23	31
	6	5	10	15
	7	4	13	17
	Total	64	127 **	191
	Sex-ratio[1]	0.5	: 1	
Natural galleries in coconut palms (6 months during Jan-Jun 97; 35 ha)	Total	122 ***	41	163
	Sex-ratio[2]	3.0	: 1	

[1] Sex-ratio within assay 4 is significantly unbalanced towards females (Wilcoxon's W-paired-test; 6 d.f.; **, $P < 0.01$).
[2] Sex-ratios of the total captures between assay 4 and gallery survey (January–June 1997) are significantly different (χ^2 test; 1 d.f.; ***, $P < 0.001$).

Collecting adults in galleries in the daytime reflected the results of the night behaviour but could not inform us about its features. Preparing artificial galleries in CPs allowed us to have the insects at a chosen place where they could be observed more easily. With nursery plants it was possible to move them when necessary. The methodology was very fruitful in providing us with original behaviour data.

At the beginning of the night, *Scapanes* males, but not females, adopted a characteristic position and behaviour at the entrance of their galleries, previously referred as 'performing'. This behaviour included the emission of a presumably rectal liquid secretion. It synchronized to sunset, lasted 1–1.5 h in Papua New Guinea. EBERHARD (1979) reported a closely related behaviour from the male neotropical Dynastid, *Podischnus agenor* (Oliv.), settled in a sugarcane gallery. The sole difference was that 'performing' *P. agenor* males were not moving their hind legs.

Male *Scapanes* behaviour obviously corresponds to calling behaviours described in various families of insects (MATTHEWS and MATTHEWS, 1978; TAMAKI, 1985; LEAL et al., 1993; LIANG and SCHAL, 1994). The calling behaviour has a sex function and is linked to the release of an attractive signal, mainly acoustic (calling songs) or chemical (pheromone). Our description from male *Scapanes* is the first report of a calling behaviour in the Dynastidae, or second (EBERHARD, 1979). A similar behaviour has been described in several dung beetles (Scarabaeidae): *Kheper* spp. and *Canthon cyanellus* Lecomte. On or nearby a dung pad, the males assume a characteristic stance with the head lowered and the abdomen raised, while they emit an abdominal secretion, which is dispersed or stuck to the legs by movements of the hind tibiae (TRIBE, 1975; BURGER et al., 1983; BELLOS and FAVILA, 1984). The peculiar behaviour observed in *Scapanes* may thus be an ancestral behavioural character common to many species of Scarabaeoidea, which ecologies have evolved differently.

The abundant chewed fibres that covered the gallery entrance and partially hid the calling males and the high sensitivity of males to plant-borne vibrations were two

factors, which had prevented previous observation of the calling behaviour. They make an effective alarm system and protection for the exposed male against predators.

The time the male *Scapanes* were calling was precisely correlated to the period of *Scapanes* flight in the field. Assays 3B–C demonstrated that males settled on CPs were attractive to both sex conspecifics. Such an effect was observed in assay 3A, although no significant difference with the others treatments could be concluded. Beetle arrivals then on the XCPs without male might have occurred because the XCPs were too close to each other or contaminated by male contact during material handling.

The nature of the male attractive signal has not been elucidated yet. Was it associated with acoustic signals emitted by the males or was it chemical? Both sex *Scapanes* were producing audible sounds, especially when two individuals were meeting, but also when handled or disturbed. The sounds appeared as a classical defensive stridulation produced in most Scarabaeoidea species by rubbing the elytra onto the dorsal part of the pygidium, as, for example, in *O. rhinoceros* and *O. nasicornis* L. (DUMORTIER, 1963; MINI, 1997). Sex songs have never been reported in Dynastidae and acoustic signals active at a range of several metres are unlikely according to the size and morphology of the beetles (COCKL and CLARIDGE, personal communication).

The male calling behaviour, which was associated with the emission of a liquid secretion strongly suggest that a pheromone is emitted. The pheromone would be an aggregation pheromone since both sexes are attracted to the males. In Scarabaeidae exhibiting such a behaviour, the secretion would contain a sex-pheromone (*Kheper* spp.; TRIBE, 1975.; BURGER et al., 1983) or has repellent properties when mixed with the dung ball (*C. cyanellus*; BELLÈS and FAVILA, 1984). No peculiar behaviour has been described in connection to the pheromone emission in the Dynastids *O. monoceros* (GRIES et al., 1994) and *O. rhinoceros* (HALLET et al., 1995; MORIN et al., 1996). Investigations are currently underway to confirm the pheromone hypothesis and identify the putative chemical signal.

Most females arriving at the male-baited XCPs had maturing oocytes, but no fully developed ones nor eggs, and spermatophore. They were young but not virgin, probably joining the males at least to mate but also to feed. This suggests that females mate several times before laying eggs. The male signal thus had a clear sex function supported by the sex-ratio of *Scapanes* caught at male-baited traps, which was unbalanced towards females.

The attraction of males to males was not elucidated. Nevertheless it fits with classical evolutionary scenarios of sexual selection and reproductive adaptation (SIGMUND, 1993). Direct sex selection based on male fighting for a settled female as described in *Dynastes hercules* (L.) (BEEBE, 1947) did not seem to be involved in *Scapanes*. Indeed females did not pioneer the CPs and males only released their attractive signal when alone in a gallery. The male selected and created a suitable site for feeding and mating: the gallery in the CP. It had a marked territorial behaviour and fought to retain or gain the possession of such a site. The male might have adapted to respond to its sex signal to gain a suitable gallery burrowed by another male through fighting, with a lesser energetic cost than burrowing the gallery for itself (EBERHARD, 1979). The males with best reproductive success would be either the best at intraspecific fights and/or at making a gallery and attracting females.

The attraction of both sexes to males and the use of traps baited with live beetles are an important step towards an improvement of *Scapanes* control. The level of catches by the method appeared very high relative to the beetle densities reported for *Scapanes* populations. This also opens a new access to the females that were not efficiently controlled by the sole gallery surveys. The discovery of a pheromone in this major pest should lead to a decisive improvement in its control and a better understanding of its biology.

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