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HOW TO BE A FIG BEETLE? OBSERVATIONS OF GROUND BEETLES (COL., CARABIDAE) ASSOCIATED WITH FRUITFALLS IN A RAIN FOREST OF BORNEO

Rainer Borcherding[1], Wilfried Paarmann[2], Samhan Bin Nyawa[3] & Hubertus Bolte[4]

[1]Norderstraße 1, D-25813 Husum, Germany
[2]Fachhochschule Hildesheim-Holzminden, FB Forstwirtschaft und Umweltmanagement, Büsgenweg 1a, D-37077 Göttingen, Germany
[3]Universiti Brunei Darussalam, Biology Department, Bandar Seri Begawan 3186, Brunei Darussalam
[4]In der Röthe 7, D-97332 Volkach, Germany

Abstract. The ground beetle assemblage (Coleoptera, Carabidae) associated with fruitfalls in a tropical lowland rain forest in Brunei Darussalam (Borneo, SE-Asia) is described. The species composition of this assemblage and the reproductive strategies of all 23 carabid species collected are analyzed. The roles of stochastic and deterministic elements in this dynamic assemblage are discussed. *Accepted 28 December 2000.*

Key words: Biodiversity, Borneo, Brunei, Carabidae, Ficus, *fruitfall, Harpalinae.*

INTRODUCTION

A percentage of every fruit crop in tropical rain forests is not eaten by seed dispersers like birds, fruitbats or monkeys, but falls to the forest floor. These fallen fruits form a sometimes rich, but always time-limited food resource. Fruit flesh, small insects feeding in it (e.g., fly maggots, male fig-wasps), and sometimes the seeds these fruits carry are potential food for fruitfall specialists.

The unpredictable occurrence of fruitfalls in space and time is a typical feature of many organic resources in tropical forests (Erwin 1979). The animal assemblage which depends on such resources is subject to a dynamic equilibrium between migration and new establishment. This raises the question, to what extent is the composition of such an assemblage determined by stochastic or deterministic processes?

The ground beetle assemblage associated with fruitfalls is a highly suitable research subject for this question: Fruitfalls, especially those of figs (*Ficus*, Moraceae), occur virtually throughout the year due to the specific pollination system of figs (Bronstein 1989, Gautier-Hion & Michaloud 1989). In addition, figs are usually abundant, species-rich, and contain small seeds that can be used by seed-eating (spermatophagous) beetles like Harpalinae (Col., Carabidae).

Triggered by interesting discoveries on similar fruitfall carabids in Brazil (Paarmann, in prep.), a comparative study was conducted in Brunei. This paper describes the results of the Bruneian study.

STUDY SITE

Topography. The study was conducted in tropical lowland rain forest in the surroundings of the Kuala Belalong Field Studies Centre (KBFSC), which is situated at the northern border of Batu Apoi National Park in Temburong District, Negara Brunei Darussalam.

The landscape is characterized by numerous sharp ridges and deep river valleys. The sides of the valleys slope at angles between 25° and 35°. The altitude is between 50 m and 200 m a.s.l.

Geology. The region consists of marine and deltaic sedimentary rocks, mainly shales, laid down in the Tertiary Period (Dykes 1994). Hard layers of "Meligan" sandstone resist erosion and form the charcteristic sharp ridges. The reddish soil is predominantly a silty clay (Ross 1994). It is poor in basic chemicals, iron-rich, and has pH values of 5.5–6.5 in the pore water (orthic acrisols / udult ultisols).

e-mail: rb@schutzstation-wattenmeer.de

Climate. The climate of the area is almost aseasonal, with day temperatures around 28° C (24.7°–29.3° C at 17:00 h) and night temperatures of 26° C (23.3°–28.9° C at 8:00 h).

The precipitation totals 4000–5000 mm per year. There are two indistinct rainy seasons a year, one in May / June and a second between September and December. Dry periods usually occur in February and August. The lowest monthly precipitation recorded during four years was in March 1992 (114 mm), the highest occurred in December 1994 (810 mm). The longest periods without any rain may usually last for ten days; the maximum rainfall recorded in one day was 210 mm (all data from daily records at KBFSC).

Vegetation. The vegetation of the study area is predominantly mixed dipterocarp forest. This forest type is extremely rich in tree species (>200 species / ha), of which many belong to the family Dipterocarpaceae (e.g., *Shorea, Dryobalanops*). Large strangler figs with leathery, xeromorphic leaves can colonize even the highest canopies of dipterocarps.

Gallery forests, characterized by ensurai (*Dipterocarpus oblongifolius*), kasai (*Pometia pinnata*), and langkap (*Arenga undulatifolia*) overhang the Belalong River (Edwards 1994). Many small fig species occur in this habitat (Borcherding & Sapoh, in prep.).

METHODS

During a six-month period (February–July 1995) all accessible hemiepiphytic and standing fig trees in the surroundings of the field center were observed for fruiting. A total of 110 figs produced 31 fruitfalls during this period. Plentiful fruitfalls of other plant families were also examined when they occurred (four cases). Fruiting trees were visited from the beginning (or detection) of the fruitfall at intervals of two to three nights. Beetles were hand collected from the leaf litter of the fruitfalls between 19:00 h and 23:00 h with the aid of a head torch. Depending on the presence and abundance of beetles, the sampling duration per tree varied from 0.5 to 1.5 hours. As the ground beetles proved to be very fast-moving and evasive, a pooter was used to pick them up. Between 60 and 95% of all observed beetles could be caught. No species appeared to be quicker or slower than the others and so the sampling can be regarded as representative. In two cases, army ants (Ponerinae) raided the areas where the leaf litter had just been turned over in the search for beetles. The ants chased up a few previously undiscovered ground beetles, but not more than 20 % of the number previously collected there.

Beetles were killed and preserved in 70 % ethanol with 10 % acetic acid. All beetles were dissected under a stereomicroscope to determine the state of gonad maturity, stomach contents, and nutritional state (deposit fat). Gonad maturity was classified according to the following scheme (Table 1) based upon the classifications of Thiele (1971) and Paarmann (1976).

The condition of maturity is more difficult to determine in males than in females, and therefore only females of maturity class III were regarded as proof of reproduction at fruitfalls.

Deposits of fat were recorded where present. Stomach contents were roughly classified. Sometimes these included chitin, oil drops, or colored fruit pulp, but usually stomach contents were missing or unspecific.

In a few cases the abdomen housed a parasitic larva (Diptera, Tachinidae) or showed sclerotized remains of a respiration "chimney" of such a parasite. These unusual observations were also noted.

TABLE 1. Gonad maturity classification scheme.

	State of reproduction	Females	Males
I	immature	ovaries very small	testes very small
II	before reproduction	ovaries larger, no eggs, no corpora lutea	testes medium
III	reproductive	ovaries large, with eggs, no corpora lutea	testes large, gland tubes full
IV	in dormancy after reproduction	ovaries large, usually no eggs, with corpora lutea	(included in category III)

RESULTS

Quantitative description of the beetle assemblage. A total of 1582 ground beetles was caught during the six-months sampling period. The genital morphology of all male carabids was examined to distinguish morphospecies. For species determination the following collections served as references: British Museum of Natural History (London), Naturhistorisches Museum (Berlin), Zoologische Staatssammlung (Munich) and the private collection of Noboru Ito (Kawanishi City, Japan). The recorded carabid fauna comprised 38 species, 15 of which (30 specimens) were rare and probably only accidental visitors not usually associated with fruitfalls. The remaining 23 species of "fruitfall-carabids" belong to 13 genera of six subfamilies (Table 2).

Diversity. The occurrence and abundances of all fruitfall carabids varied considerably between individual fruitfalls. Eight of 35 fruitfalls were free of carabids. At the other sites, between one and 730 beetles were caught (41.5 ± 129 on average). The highest catch rate at a single fruitfall was 180 beetles/hour, indicating an enormous densitiy of several beetle species. This fruitfall (*Ficus sundaica*, tree No. 3) probably housed 3000–5000 adult carabids at a time, about ten per square meter.

The maximum diversity at a fruitfall was 23 species (including 4 accidental visitors), collected in 5.5 hours over six nights. The average number of fruitfall species per inhabited fruitfall was 4.5 (± 5.1), with an average of 1.5 (± 3.1) reproducing species.

It was noticeable that species composition and abundance varied widely among fruitfalls, even within one species of fig. Possible reasons for this phenomenon are discussed later. Table 3 gives an overview of all fruitfalls recorded and of the associated beetles.

Distribution patterns and ecological groups (guilds). The distribution of most carabid species over different fruitfalls shows noticeable aggregation. For example, 94 individuals of *Lampetes* sp. 10 were caught, 93 of them at just two sites. The opposite seems to be the case for *Hyphaereon louwerencei*: this species was found

TABLE 2. The fruitfall carabid community at Kuala Belalong (excluding "visitor" species).

Taxon	Subfamily	Females/Males	Record sites	Reproduction sites
Lampetes sp. 1	Harpalinae	132 / 117	13	4
Lampetes sp. 1a	Harpalinae	39 / 103	5	2
Lampetes sp. 10	Harpalinae	32 / 62	3	2
Lampetes sp. 25	Harpalinae	31 / 50	4	2
Lampetes sp. 25a	Harpalinae	2 / 4	2	1
Hyphaereon louwerencei	Harpalinae	80 / 137	20	9
Hyphaereon borneensis	Harpalinae	46 / 47	11	5
Harpaloxenus sakaii	Harpalinae	4 / 0	2	1
Coleolissus ohkurai	Harpalinae	20 / 24	7	–
Coleolissus similis	Harpalinae	14 / 12	9	–
"*Abacetus*" sp. 30	Harpalinae	5 / 8	5	2
"*Colpodes*" sp. 3	Agoninae	9 / 33	10	2
"*Colpodes*" sp. 3a	Agoninae	33 / 144	7	3
Colpodes sp. 18	Agoninae	41 / 21	5	3
"*Agonum*" sp. 8	Agoninae	21 / 26	13	3
"*Notagonum*" sp. 22	Agoninae	3 / 5	1	–
Arhytinus sp. 19	Agoninae	16 / 20	9	3
Arhytinus sp. 23	Agoninae	11 / 21	4	1
Arhytinus sp. 24	Agoninae	6 / 3	4	3
cf. *Holosoma boettcheri*	Oodinae	6 / 17	12	1
cf. *Coptodera picta*	Lebiinae	10 / 16	4	4
Perigona aff. *ludovici*	Perigoninae	9 / 6	10	5
Pentagonica cf. *blanda*	Scopodinae	2 / 4	5	–

TABLE 3. Carabid numbers at fruitfall sites at Kuala Belalong. "Fruitfall beetles" are regularly associated with fruitfalls (five or more specimen recorded), "visitor species" are rare, probably accidental visitors (n < 5). "Reproducing species" are those fruitfall beetles, of which mature females were caught at fruitfall sites. The catchrate per hour is an indicator of relative carabid density. *Ficus* determination was not always clear, e.g., *F. sundaica* occurred in several "forms" with different fruit shapes (A, B, C).

Tree species	Tree no.	Fruitfall beetles		Reproducing species		Visitor species		Catchrate
		species	*specimen*	*species*	*specimen*	*species*	*specimen*	beetles/hr
F. microcarpa	5a	5	6	1	1	1	1	3.5
F. microcarpa	14a	1	1	-	-	-	-	1.0
F. virens	36	6	10	-	-	1	1	7.3
F. binnendijkii	13.2	-	-	-	-	-	-	-
Medium-sized figs (10–20 mm fruit diameter) *Ficus* subgenus *Urostigma*								
F. sundaica A	3	19	726	12	625	4	4	71.2
F. sundaica A	13	1	2	-	-	-	-	2.0
F. sumatrana	9	7	30	1	21	2	2	9.1
F. "delosyce"	25	13	47	2	7	1	1	32.0
F. consociata	4b	2	3	-	-	-	-	0.8
F. pellucido-punct.	2b	5	34	-	-	1	1	14.0
F. subgelderi	12a	9	50	-	-	3	3	13.3
F. subtecta	2a	6	23	3	20	-	-	11.5
F. subtecta	20aE	1	1	-	-	-	-	2.0
F. subtecta	24	2	8	-	-	-	-	4.0
F. subtecta	24a	1	2	-	-	-	-	2.0
F. subtecta	2190	-	-	-	-	-	-	0.0
F. lowii	JT	-	-	-	-	-	-	-
Large figs (20–30 mm fruit diameter) *Ficus* subgenus *Urostigma*								
F. dubia	38	3	8	3	8	-	-	8.0
F. sundaica B	BB1	-	-	-	-	-	-	-
F. sundaica C	45	2	3	1	1	-	-	3.0
Very large figs (30–40 mm fruit diameter) *Ficus* subgenus *Urostigma*								
F. subcordata	8a	18	314	14	281	4	5	58.0
F. stupenda	14	12	59	3	20	1	2	15.3
F. stupenda	18	12	20	4	11	-	-	5.7
F. stupenda	42	10	32	-	-	3	3	11.7
F. stupenda	8	-	-	-	-	-	-	0.0
Other *Ficus* subgenera of different fruit size								
F. heteropleura	Kua	2	5	1	4	1	1	6.0
F. vasculosa	S1	5	7	1	4	2	2	9.0
F. vasculosa	S2	6	22	3	17	-	-	4.4
F. urnigera	4c	-	-	-	-	-	-	-
F. parietalis	River	-	-	-	-	-	-	0.0
F. hemsleyana	Tudal	-	-	-	-	-	-	-
F. sinuata	B1	-	-	-	-	-	-	0.0
Other plant families								
Castanopsis (Fagaceae)	x1	1	1	-	-	-	-	2.0
Ryparosa (Flacourtiac.)	x2	2	6	-	-	-	-	1.3
xy	x3	3	4	-	-	-	-	4.0
Myristicaceae	x4	7	71	5	34	2	3	29.6

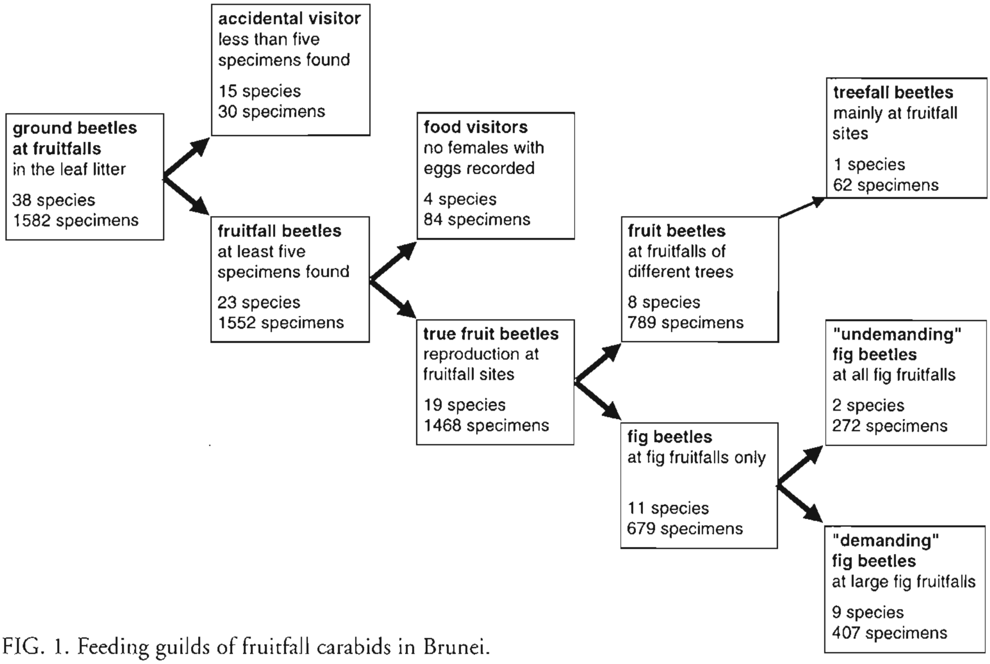

FIG. 1. Feeding guilds of fruitfall carabids in Brunei.

at 20 sites and was reproductive at 9 of them at least. Nevertheless, more than half of all individuals were found at the two main attractive fruitfall sites. The rest were scattered over 18 less attractive sites.

Judging from distribution of species, and in view of the dissection data (deposited fat and stomach contents) and of some laboratory observations on food preferences, the following species groups of carabids at fruitfall sites in Brunei can be distinguished:

Reproducing seed-eaters: beetles and larvae at fig fruitfalls feeding on fig seeds and small insects (and fruit flesh?).

Reproducing omnivores: beetles and larvae at fruitfalls feeding on small insects and fruit flesh.

Visiting omnivores: beetles at fruitfalls feeding on small insects and fruit flesh.

An even finer ecological classification can be determined from a closer examination of the host tree preferences: some carabid species appear at many different fruitfalls of different plant families (e.g., *Hyphaereon louwerencei*, "*Colpodes*" sp. 3). Others are restricted to fig fruitfalls (*Lampetes* sp.1) or to certain fig fruitfalls only (e.g., *Lampetes* sp.1a, *Lampetes* sp.10). One species (*Colpodes* sp.18) was found reproducing both at fruit- and at treefall sites.

There seem to be different degrees of specialization in feeding guilds (Fig.1), e.g., between "undemanding" fig beetles, occurring at many fig fruitfalls, and "demanding" fig beetles, restricted to certain fig fruitfalls.

Fruitfall amount and duration as limiting factors for beetles. To understand the differences in attractiveness for beetles it was necessary to quantify and characterize the individual fruitfalls. A quantification of falling fruits is not easy, as the tree canopy is uneven and a large number of samples is necessary to obtain accurate data (Coates-Estrada & Estrada 1986, Chapman *et al.* 1992). Furthermore, the fruit pulp accumulated in fruit traps is not easy to quantify, especially when it is mixed with animal droppings, empty fruit bracts, and rainwater. In this study, single funnel-shaped collecting trays of 1 m^2 were used to get rough assessments of fruitfall durations, intensity, and weight.

The contents of the collecting trays were emptied at intervals of 2–3 days or longer. Whole fruits, fruit flesh, and empty bracts (the latter probably from fruits eaten by vertebrates in the canopy) were counted. Some quantitative data on fruitfalls are compiled in Table 4.

TABLE 4. Fruitfall duration and amount recorded at Kuala Belalong

Ficus species and tree no.	Date of fruitfall	Duration (days)	Fruits per m²	Estimated total fruitfall	Estimated fruitfall weight	Seed [1] share
Small figs, subgenus *Urostigma*: (7 mm fruit diameter)						
F. microcarpa (5a)	15.–27.2.	13	420	21,000	10 kg	6.5 %
F. virens (36)	28.6.–22.7	25	1,900	150,000?	75 kg	3.4 % [2]
Medium-sized figs, subgenus *Urostigma*: (10–20 mm fruit diameter)						
F. sundaica A (3)	30.3.–23.4.	25	550	250,000	250 kg	3.2 %
F. sumatrana (9)	10.6.–20.6.	11	45	3,600	4 kg	4.6 %
F. consociata (4b)	30.3.–12.4.	14	75	6,300	5 kg	5.9 %
F. pelluc.-pct. (2b)	?9.–17.2.	9	200?	10,000?	10 kg?	? [2]
F. subgelderi (12a)	15.2.–1.3.	15	170	1,300	3 kg	13.6 %
F. subtecta (2a)	12.7.–25.7.?	14	200?	19,000?	40 kg	3.2 % [3]
Large figs, subgenus *Urostigma*: (20–30 mm fruit diameter)						
F. dubia (38)	15.6.–15.7.	31	10 (70)	5,600?	45 kg?	38.3% [4]
Very large figs, subgenus *Urostigma*: (30–40 mm fruit diameter)						
F. subcordata (8a)	26.4.–6.5.	11	10?	1,800?	35 kg?	15.7 %
F. stupenda (14)	28.3.–6.4.	10	20	4,800	100 kg	14.4 %
F. stupenda (18)	28.4.–4.5.	7	20	3,400	70 kg	13.2 %
F. stupenda (8)	30.5.–5.7.	10+8	5+7	3,800	75 kg	18.0% [5]
Other *Ficus* subgenera						
F. vasculosa (S2)	15.3.–24.3.	10	120	9,600	20 kg	28.2 %

[1] Percentage of seeds (excluding galls) from all female flowers.
[2] The beginning of fruitfall was not recorded.
[3] The end of fruitfall was not recorded.
[4] Both hanging and fallen fruits were almost completely eaten by vertebrates.
[5] Two separate fruitfalls with a gap of 16 days between.

Maturation and lifespan. The problems of survival and lifespan are important for animals that depend on irregular reproductive opportunities. Fruitfall beetles need to live long enough to find and colonize several fruitfalls. As field data from marking experiments are not available in this case to calculate real lifespans, laboratory observations and relative shares of age classes of dissected beetles are used here to make estimates.

Lampetes sp.1 has been kept in culture in Göttingen for several generations since March 1995. With 12 hours light per day and at 21°/27° C the beetles

- reach maturity (hardening of the exoskeleton) after 15 (10–20) days
- reach sexual maturity (gonad state III) after 40 (30–50) days,
- die after 250 (110–360) days.

The duration of these developmental stages should reflect the relative proportions of age classes of beetles caught in the field. However, optimal food supply in the laboratory possibly accelerates reproduction and shortens life span. Table 5 shows age class proportions from the field and laboratory for *Lampetes* sp.1.

The occurrence of immature beetles of the genus *Lampetes* is slightly lower in the field (4.9 %) than in captivity (6 % of lifespan). Thus the lifespan in the field may be longer (300 or more days) than under culture conditions (250 days on average).

Transport eggs. In several species the ovaries of mature females contained one or two fully grown eggs, while the corpora lutea, which indicate gonad dormancy and egg absorption, were already present. This phenomenon was also observed in *Notiobia* species (Carabidae), specialized on fig seeds in Brazil (Paarmann, pers. obs.). This can be interpreted as an adaptation to the extremely short availability of food resources for larvae. A female with such preformed "transport eggs" can oviposit immediately on arrival at a fruitfall and has a chance to reproduce before the dormancy of her gonads is terminated. Larval development from oviposition until pupation lasts at least 20 days in brazilian fig beetles (Paarmann in prep.).

Females with transport eggs arriving at a fruitfall are unlikely to be collected since they should oviposit within minutes or hours. Females with newly formed transport eggs, and due to leave the fruitfall, may be expected to be found towards the end of a fruitfall.

Table 6 lists all females with transport eggs in relation to the "age" of the respective fruitfall.

In fact 16 of 18 records of transport eggs occurred 12 or more days after the beginning of the respective fruitfalls, when the end of fruitfall was near and further oviposition at that fruitfall would have served no purpose. Almost all of the females with transport eggs (18 of 20) possessed deposited fat.

Parasites. The occurrence of parasites was, with two exceptions, restricted to carabids of the subfamily Harpalinae. Between one and three ovipositions of the parasite were found to occur in single beetles. In many cases (17 of 31) only a sclerotized tube inserted in the abdominal tergites 3 or 4 indicated that a parasitic larva (Diptera, Tachinidae?) had inhabited a beetle. In some cases the thickening seemed to contain remains of the parasite (or a shed skin?), but in most cases it was clearly just the scar of the parasitic respiration opening. This indicates that parasitism is not, or not always lethal. Infestation can occur soon after hatching, demonstrated by several examples of parasitized immature beetles. But also older beetles can become parasitized as shown by several female *Lampetes* sp. 1a in gonad dormancy (after reproduction). A feature all parasitized beetles had in common was that they were not ready for reproduction, although some were well fed with large amounts of deposited fat. Malnutrition seems not to be a consequence of parasitic infestation. It is not clear if a beetle can reproduce after the parasite is gone, as no previously parasitized females with eggs were found.

TABLE 5. Frequency of development stages of "wild" fruitfall-beetles (%) in relation to development stage durations of *Lampetes* sp.1 in captivity.

Species (n > 30)	Immature (%)	Gonad maturity I	Gonad maturity II	Gonad maturity II+IV	Unknown
Lampetes sp. 1	2.8	15.6	29.7	44.2	7.6
Lampetes sp. 1a	4.9	14.1	25.4	54.9	0.7
Lampetes sp. 10	4.3	11.7	43.6	40.5	–
Lampetes sp. 25	7.4	18.5	32.1	42.0	–
Hyphaereon louwerencei	–	4.2	47.4	47.4	0.9
Hyphaereon borneensis	–	7.5	60.1	30.1	2.2
Coleolissus ohkurai	–	22.7	59.1	9.1	9.1
"*Colpodes*" sp. 3	–	7.1	23.8	66.7	2.4
"*Colpodes*" sp. 3a	–	5.1	22.7	72.3	–
"*Colpodes*" sp. 18	–	6.4	41.9	51.6	–
"*Agonum*" sp. 8	8.5	17.1	29.8	38.3	6.4
Arhytinus sp. 19	–	–	11.1	88.8	–
Arhytinus sp. 23	–	–	21.9	75.0	3.1
all species	2.1	10.3	35.2	50.0	2.5
Laboratory observations:					
Lampetes sp.1 (%)	6.0	10.0	84.0		–
duration (days)	15	25	210		–

TABLE 6. Occurrence of transport eggs in relation to fruitfall age.

Individual beetle females with transport eggs		Number of transport eggs per female	Females with transport eggs (% per species)	Day of fruitfall
Lampetes	sp.1	1	3.2 %	16th of 25
	sp.1	2		18th of 25
Lampetes	sp.1a	1	5.2 %	14th of 25
Lampetes	sp.10	1	23.0 %	16th of 25
	sp.10	1		16th of 25
	sp.10	1		16th of 25
	sp.10	1		16th of 25
	sp.10	2		12th of 14
	sp.10	2		12th of 14
Lampetes	sp.25	1	10.5 %	16th of 25
	sp.25	1		16th of 25
Hyphaereon	*louwerencei*	1	3.6 %	?
	louwerencei	1		?
Hyphaereon	*borneensis*	1	4.0 %	18th of 25
"*Colpodes*"	sp. 3 + 3a	1	8.1 %	6th of 14
	sp. 3 + 3a	1		8th of 25
	sp. 3 + 3a	1		18th of 25
	sp. 3 + 3a	1		21th of 25
	sp. 3 + 3a	3		21th of 25
	sp. 3 + 3a	4		23th of 25

The only case of parasitism in the subfamily Agoninae was observed in a female "*Colpodes*" sp. 3, which contained 16 small parasitic larvae, possibly of a chalcidoid wasp.

The degrees of parasitism are indicated in table 7. It is obvious that there are interspecific differences and that males are more frequently infested than conspecific females.

TABLE 7. Abdominal parasites (Diptera, Tachinidae?) in fruitfall carabids.

Species name	Parasitism in females				Parasitism in males				Total
	%	n	m	md	%	n	m	md	%
Harpalinae									
Lampetes sp.1	1,5 %	2	2	–	4,3 %	5	5	1	2,8 %
Lampetes sp.1a	5,1 %	2	–	2	5,8 %	6	1	5	5,6 %
Lampetes sp.25	3,2 %	1	1	–	8 %	4	4	3	6,3 %
Hyphaereon louwerencei	0 %	–	–	–	1,4 %	2	1	2	0,9 %
Hyphaereon borneensis	2,1 %	1	1	–	6,5 %	3	–	4	4,1 %
Oodinae									
Holosoma boettcheri	0 %	–	–	–	5,9 %	1	1	–	4,2 %

% = percentage of parasitized beetles
n = number of parasitized beetles
m = number of life maggots
md = number of dead maggots

DISCUSSION

With 23 species so far recorded, the ground beetle community of fruitfall sites in Brunei is very diverse. The question is: why?

Has extreme specialization led to a competition-reduced coexistence of all species (deterministic principle), or do unpredictable events and instability prevent competition and allow for a diverse community (stochastic element)?

A definitive answer is not yet clear, but discussion of some of the preliminary findings may elucidate the problem.

The choice of suitable reproduction sites is obviously a central question for fruitfall beetles. Most recorded species used less than 10% of all fruitfalls for reproduction (on average 2.3 ± 2.0 of 35), although they were present at many more sites (7.2 ± 4.6 of 35; see Table 2). As 40 % of all fruitfalls housed at least one reproducing species, many fruitfalls seem to be suitable for beetle reproduction. One carabid (*Hyphaereon louwerencei*) in fact reproduced at 25 % of all fruitfalls. Nevertheless a strict preference was shown by most species, and 2/3 of all individuals preferred just two individual fruitfalls (3, 8a). Six of 19 species reproduced only at these two sites, while a widespread species ("*Agonum*" sp. 8) strictly avoided both of them. All these facts indicate selectivity and hence provide evidence of deterministic processes.

Enormous qualitative and quantitative differences were found between the carabid communities of different fruitfalls, with numbers of species and specimens varying widely (Fig. 2). This indicates the absence of regulating factors, and hence a predominance of stochastic elements.

Conspecific fruitfalls were not always equally attractive for beetles. For example, in *Ficus sundaica* one fruitfall rendered 730 beetles (catch rate 71.2 per hour), while a second delivered only two beetles (catchrate 2.0/h). This also suggests unpredictable, stochastic processes.

A possible explanation for the beetles' preferences could be quality and size of figs and their seeds. However, a comparison of the two most attractive fruitfalls (*F. sundaica, F. subcordata*) shows that these two figs have little in common (Table 8).

One aspect in particular appears to be important: the amount of seed, which probably plays an important role for *Lampetes* spp., particularly for *Lampetes* sp.1. This species prefers fruitfalls with medium-sized seeds (Fig. 3) and, in contrast to *Hyphaereon louwerencei*, does not play a role at the fruitfall of *F. subcordata*. The occurrence of *Lampetes* sp.1 is probab-

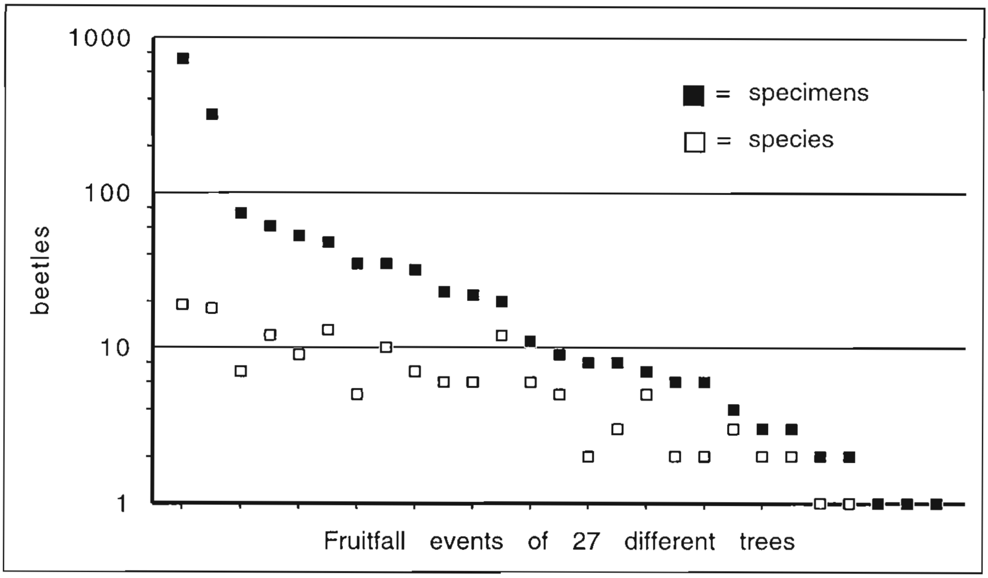

FIG. 2. Numbers of specimens and species of fruitfall beetles at different fruitfalls.

TABLE 8: Features of two fruitfalls of highest attractiveness for beetles.

Feature	*Ficus sundaica*	*Ficus subcordata*
fruitfall duration	25 days	11 days
fruitfall area	450 m^2	180 m^2
fruitfall amount	250 kg	35 kg ?
fruit size	14 x 14 mm	33 x 39 mm
seed size	1.5 mm	2.5 mm
seed share	3.2 %	15.7 %
dropped seeds / m^2	3500	4500
fruit predators	barbets	hornbills, gibbons
fruitfall carabids (n)	730	310
carabid species (n)	19	18
reproducing species (n)	12	14
beetles with deposited fat	66 %	70 %

ly influenced by the seed contents of figs and by the activity of seed-eating bugs (Het., Lygaeidae). The other *Lampetes* species were only found at fruitfalls with high beetle densities (catch rates), independent of seed size. In the genus *Lampetes* there are clearly specializations, thus indicating deterministic elements.

Fruitfall durations might be expected to influence the beetles' preferences, as longer durations should favor larval development. In Fig. 4, fruitfall durations are compared with beetle abundances at the respective fruitfalls (measured as catch rate). Rough correlations exist between these two factors, but fruitfall duration seems not to be the only decisive factor.

A third aspect that might influence reproductive success of carabids is the amount of fallen fruit. Fig. 5 shows a comparison between beetle abundance (catch rate) and estimated amount of fruit on the ground. Obviously there is no strict correlation between the fruit amount and beetle choice. One extraordinary case was the very attractive fruitfall of *Ficus subcordata*, which had a relatively small crop. In this case the figs contained a yellow oil, which was found in many stomachs and led to the very good nutritional state of most beetles caught. Hence quality can obviously compensate for quantity, and the "nutritional value" of a fruitfall (fruit, oil, or meat) may

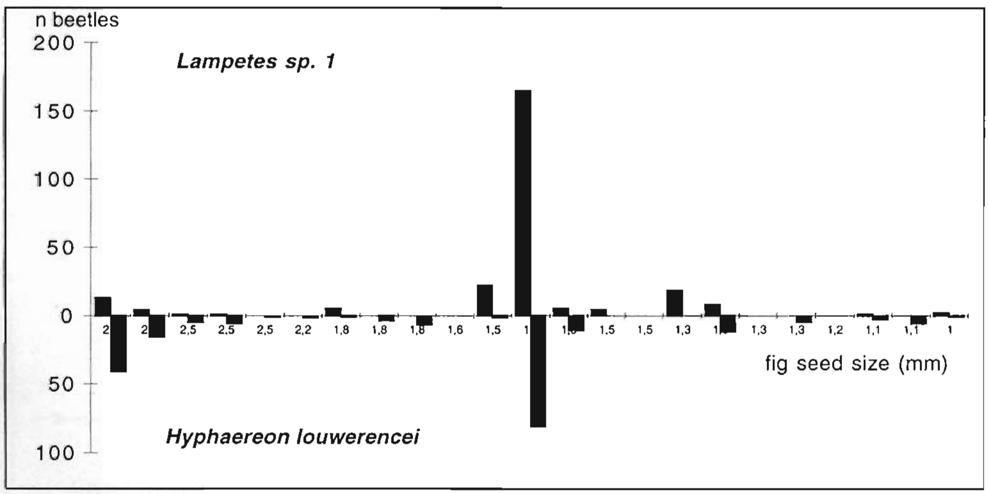

FIG. 3. Abundance of *Lampetes* sp.1 and *Hyphaereon louwerencei* at fig fruitfalls of different seed size.

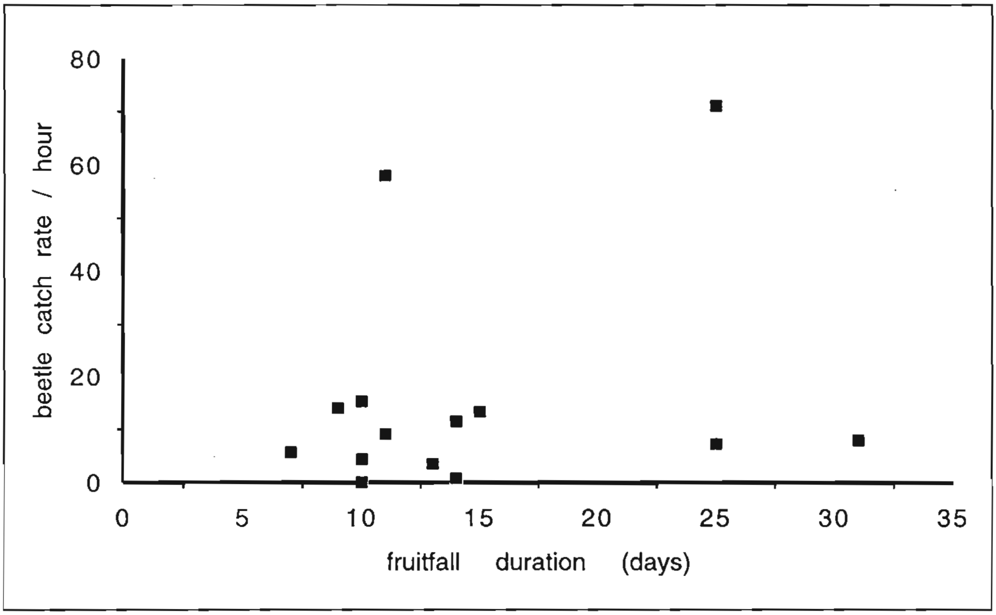

FIG. 4. Beetle abundance (catchrate / hour) in relation to fruitfall duration (days).

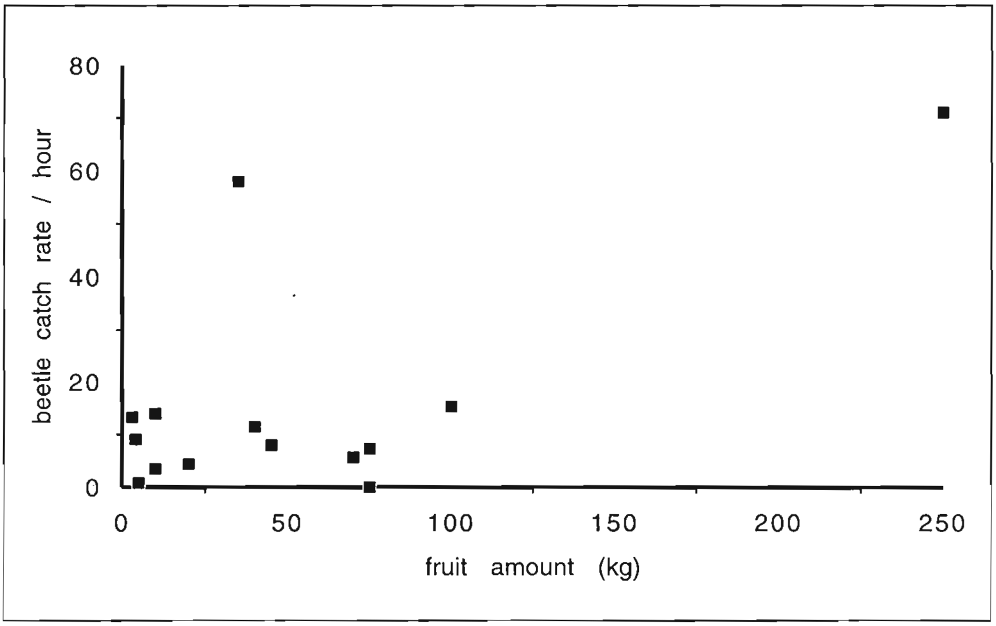

FIG. 5. Beetle abundance (catch rate / hour) in relation to fruit amount on the ground.

be regarded as a determining factor for many fruit beetles.

The unpredictability of food supply, and hence opportunities for reproduction, requires temporal and spatial flexibility in fruitfall beetles. The occurrence of gonad dormancy and of transport eggs, in combination with a long lifespan, allow for the former. High mobility (flight) and a good orientation and discrimination ability (very selective occurrence of *Lampetes* spp.) guarantee spatial flexibility. In one instance, a female *Lampetes* sp. 1 was found under a fig tree one day before the fruitfall actually started! One may speculate upon the factors which lead (night-?) flying carabids to fruitfalls. For fig-beetles it could be the odor of ripe figs. For fruitfall generalists it is probably the smell of rotten fruit. Aggregation pheromones could play a role in species which tend to aggregate at specific fruitfalls (*Lampetes* sp. 1a, 10, 25, 25a). Parasite pressure may be a reason why the whole community is nocturnal.

In conclusion the following can be stated: The ground beetle community associated with fruitfalls in Brunei does not depend on chance events only. There exist clear preferences for large fruitfalls of long duration and of high nutritional value. Small white figs are usually not attractive. At least one carabid species shows distinct specializations (*Lampetes* sp. 1 for medium-sized fig seeds). Intraspecific aggregations were observed in several species (*Lampetes* sp.1a, 10). Even interspecific effects occur (exclusion of *Agonum* sp. 8 from "crowded" fruitfalls).

On the other hand a large proportion of the community are fruitfall generalists: Five species occurred at every second fruitfall. Many species are not specialized upon specific fruits (all Agoninae and *Hyphaereon*). This enables them to use large fruitfalls of rare plants (like *Ficus subcordata*) as critical stepping stones for reproduction and nutrition. In several species all females had fully developed ovaries, whereas in others the females carry "transport eggs". Both features are adaptations to unpredictable reproduction opportunities. All beetles examined are omnivores and consume small insects and fruit pulp.

The fruitfall community studied here is determined equally by stochastic and deterministic elements. Specializations do occur, but generalistic behavior and chance events play an important role in the maintenance of this species-rich community in the tropical rain forest.

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