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The structure of ground beetle assemblages (Coleoptera: Carabidae) at fig fruit falls (Moraceae) in a terra firme rain forest near Manaus (Brazil)

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ABSTRACT. The carabid beetle assemblage found feeding on fig fruit falls at night was studied in a terra firme rain forest near Manaus (Amazonia) from July 1991 to August 1996. A total of 8926 carabid beetles were collected on 64 fruit falls from 10 fig species. The most abundant genus was *Notiobia* with eight species, *N. pseudolimbipennis* being the most abundant. The *Notiobia* species comprised 92% of all specimens collected and all feed on small fig seeds. Their species abundance patterns varied considerably between individual fruit falls and during the course of a single fruit fall. However, the species abundance patterns for all *Notiobia* at all observed fruit falls for each of the two commonest fig species (*Ficus subapiculata*, *F. guianensis*), as well as for fruit falls of the remaining fig species, were very similar. Through feeding and breeding experiments and observations of reproductive success by dissection of females, only two of the eight *Notiobia* species were found to be specialized fig seed feeders, being able to reproduce only on fig fruit falls. The remaining six species of this genus use fig fruit falls as alternate hosts or 'stepping stones' between fruit falls of their host trees, which are widely separated both in time and space.

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INTRODUCTION

Carabid beetles are one of the best known, taxonomically and ecologically, of all temperate insect groups. In part this is because they are easy to collect and observe. For example, pitfall trapping (Thiele 1977) collects large numbers of ground-dwelling Carabidae in temperate forests. In such forests many large wingless species of *Carabus* and *Abax* are more or less uniformly distributed, due to a similar distribution of their prey (insects, snails, earthworms). Similar conditions were found for Carabidae in tropical montane forests of Central Africa (Paarmann 1974).

In lowland tropical rain forests carabid abundance appears to be very low and the distribution of individuals is extremely patchy. The carabid fauna is entirely different at the species level and almost completely different at the generic level from temperate faunas. Sampling methods commonly used in temperate regions usually fail in tropical forests; pitfall trapping usually only catches a few individuals of a comparatively high number of species (Paarmann 1974). The distribution of carabid assemblages usually reflects the patchy availability of food resources. Erwin (1979), for example, first described the typical migration movements of forest ground dwelling Carabidae in rain forest in Panama where they build temporary communities in patches of fruit, blossom or leaves that have fallen to the ground. These decaying piles of plant matter disappear rapidly within weeks and after this the adult beetles and their juvenile offspring emigrate to another fall of leaves or other vegetable matter.

Most carabid beetles are considered to be predaceous as adults and larvae. However, a few species are partially or completely herbivorous and little is understood about assemblages of such species, particularly in tropical rain forests where food resources are frequently highly limited both spatially and temporally. We have studied such carabid assemblages associated with accumulations of fruit under fig trees and other tree species in a terra firme (non-flooded) rain forest near Manaus (Brazil). Because such fruit falls are so sparsely distributed in rain forest and often last just a few weeks, we postulate that the species composition of such an assemblage may be highly influenced by stochastic processes (cf. Linsenmair 1990). We found carabids feeding on the fruit falls of figs (*Ficus*, Moraceae), species belonging to the genera *Bellucia, Loreya* and *Miconia* (Melastomataceae), *Vismia* (Clusiaceae) and *Coussapoa* (Cecropiaceae). Here the carabids feed on the small seeds of these species and on the other invertebrates that are found in the fruit piles. In this paper we describe the structure of these carabid assemblages at *Ficus* fruit falls based on data collected over a 5-y period from July 1991 to August 1996.

METHODS

Study site and sampling

The study site is located within the Reserva Florestal Adolpho Ducke ('Reserva Ducke'), about 26 km northeast of Manaus (2°55′S, 59°59′W), and managed by the National Institute for Amazonian Research (INPA), Manaus, Brazil. The year is divided into a rainy season (December–May: average precipitation 1550 mm) and a dry season (June–November: average precipitation 550 mm), but each month has significant precipitation (see Ribeiro & Adis 1984, Ribeiro & Villa Nova 1979). In 1994, mean annual maximum temperature in the Reserva Ducke was 31.4 °C (ranging from 29.4–33.2 °C); the mean annual minimum temperature was 22.1 °C (ranging from 21.4–22.6 °C); and the mean annual temperature amplitude was 9.3 °C with a maximum in August (11.4 °C) and a minimum in January (7.1 °C).

Ground beetles (Carabidae) on fig fruit falls are strictly nocturnal. At night they are active in the leaf litter surface and easy to collect by hand. We sampled all carabid beetles observed at a fruit fall over a 2-h period or less if none were found in the first 20 min with the aid of torches and later used Koehler head lamps, which are brighter and enabled us to use both hands for collecting.

Determination of gonad maturity and breeding experiments

Some of the beetles were dissected to determine the state of gonad maturity. The different stages of maturity are summarized here in two categories: (1) mature: females with ripe eggs in the ovaries; males with full developed accessory glands – filled with secretion, and visible sperm bundles (spermiozeugma); (2) immature: females without ripe eggs; males with small accessory glands – without secretion, and not yet fully developed sperm bundles. From this latter group we subtracted the newly hatched (teneral) beetles. Most of them represent the offspring of the assemblage and appear at the end of the fruit fall. They serve as indicators of successful reproduction. A few beetles were parasitized by Diptera larvae and these were all immature.

To find out which of the common fruit fall dwelling species are able to develop successfully with only fig seeds as food, we bred them, either directly at the field station in Reserva Ducke under natural temperature conditions or in Göttingen (Germany) under controlled laboratory conditions (12 h/12 h light/dark cycle and a temperature cycle with 15 h of 21 °C and 9 h of 27 °C). For these experiments, first instar larvae were isolated individually in glass tubes (7.5 cm high, 2.5 cm diameter) filled with peat to a depth of 5 cm and closed with a punctured plastic lid. They were fed only with fig seeds. Predatory mites are a constant problem in cultures and cause a high death rate at the pupal stage. Therefore, for this experiment, development was considered complete when the larvae reached the pupal stage.

RESULTS

Composition of the fig fruit feeding carabid community

Table 1 lists the fig tree species fruit falls monitored for carabid beetles and includes their names and the number of fruit fall events observed for each species. We found carabid beetles at all but three of these 64 fruit fall events (one of each of *F. albert-smithii*, *F. donell-smithii* and *F. mathewsii*). The number of beetles caught varied between 2 and 1052 for the remaining 61 fruit falls. The highest number of fruit fall events observed for any single tree was six.

A total of 8926 specimens of 36 species of Carabidae were collected (Table 2). We were unable to identify the genus for four species and 12 individuals were not identified to morphospecies but were probably predatory species. The carabid fauna of South America is so poorly known that not surprisingly almost all of the species collected were new to science or were impossible to name without taxonomic revisions of the groups concerned. Eight species are seed feeders and belong to the genus *Notiobia*. Three of the *Notiobia* species, formerly unknown to science, *N. glabrata*, *N. maxima*, *N. pseudolimbipennis*, have been described by Arndt (1998).

The eight seed feeding species represent 92% of the individuals collected (Table 2). The other 28 species are almost certainly all predatory, based on their known biology and their mouthparts, and probably feed on the insects feeding on the fleshy parts of the fruits and on the seed-eating carabid larvae. Together they total only 8% of the individuals. Only seven of these species were represented by more than 10 individuals and can be regarded as part of this community. The other 21 species can be regarded as tourists (cf. Moran & Southwood 1982).

The dominance structure of the *Notiobia* species, based on all collected data and separated for the two most common fig species (*F. subapiculata* and *F. guianensis*) as well as the group of remaining fig species, is given in Table 3.

Table 1. Number of fruit falls for different *Ficus* species studied at the Reserva Ducke, Amazonia, with their abbreviations as used in Figure 2.

Species of *Ficus*	Abbr.	Number of fruit fall events
F. subapiculata	Fs	19
F. guianensis	Fg	16
F. guianensis complex	Fgc	7
F. mathewsii	Fm	6
F. donell-smithii	Fds	5
F. greiffiana	Fgr	5
F. albert-smithii	Fas	2
F. hebetifolia	Fh	2
F. pakkensis	Fpk	1
F. panurensis	Fpn	1

Table 2. Numbers of individuals of carabid species collected at 61 fig fruit falls at Reserva Ducke, Amazonia. The genus is not known for four of the species. Unknown spp. were not identified but probably represent some of the predatory species listed.

Species	Number
Seed feeding species	
Notiobia pseudolimbipennis	4611
N. flavicinctus	1129
N. glabrata	1288
N. nebrioides	816
N. umbrifera	191
N. maxima	126
N. aulica	62
N. disparilis	4
Predatory species	
Loxandrus sp. 1	307
Coptodera sp. 1	116
Coptodera sp. 2	91
Loxandrus sp. 2	45
Loxandrus sp. 3	40
Abaris sp. 1	24
Abaris sp. 2	12
Loxandrus sp. 4	9
Apenes sp. 1	5
(Sp. 9)	4
Apenes sp. 2	4
Pelmatellus sp. 1	4
Apenes sp. 3	3
Taeniolobus sp.	2
Apenes sp. 4	2
Apenes sp. 5	2
Apenes sp. 6	2
Apenes sp. 7	2
Apenes sp. 8	2
(Sp. 110)	2
Loxandrus sp. 5	2
Diploharpus sp.	1
(Sp. 50)	1
(Sp. 84)	1
Loxandrus sp. 6	1
Apenes sp. 9	1
Apenes sp. 10	1
Apenes sp. 11	1
Unknown spp.	12

The dominant beetle species in all cases is *N. pseudolimbipennis*. The abundance distribution of the beetle assemblages for the complete data set are quite similar by a chi-squared test ($\chi^2 = 3.41, 2.46, 2.82$, df = 6, P = 0.756, 0.873, 0.831, not significantly different) to those from the data when divided into fig species or a species group.

Abundance distribution of Notiobia *at fruit falls*

At different fruit falls of the same tree, and/or the same tree species, the abundance of the four most common *Notiobia* species varied considerably from fruit fall to fruit fall (Table 4). We tested these variations against an equal distribution by using the chi-squared test. At *Ficus subapiculata* fruit falls (Table

Table 3. Dominance structure (%) of seed-feeding *Notiobia* species on fig fruit falls at Reserva Ducke, Amazonia derived from all collected data or separated for the two most common *Ficus* species and for the group of remaining species.

	Ficus species			
Notiobia species	*F. guianensis*	*F. subapiculata*	Other *Ficus* spp.	All
N. pseudolimbipennis	61.0	53.9	49.4	56.0
N. glabrata	14.5	16.4	16.8	15.7
N. flavicinctus	13.6	11.8	16.3	13.7
N. nebrioides	7.1	10.8	13.9	9.9
N. umbrifera	2.6	2.6	1.5	2.3
N. maxima	0.9	2.6	1.1	0.8
N. aulica	0.3	1.7	0.9	1.5
N. disparilis	0.0	0.1	0.0	0.1
No. of fruit fall events	16	19	26	61

4a) they were significantly different for two of the beetle species: *N. nebrioides* ($\chi^2 = 48.2$, df = 4, $P < 0.001$) and *N. maxima* ($\chi^2 = 13.7$, df = 4, $P < 0.001$), but not significantly different for *N. pseudolimbipennis* ($\chi^2 = 3.67$, df = 4, P = 0.453), *N. glabrata* ($\chi^2 = 4.0$, df = 4, P = 0.406), *N. flavicinctus* ($\chi^2 = 5.65$, df = 4, P = 0.227). By using the Kolmogorov–Smirnov test, significance was found for four of the tested species (P from < 0.001 to 0.041, z from 4.025 to 1.395) with the exception of *N. glabrata* (z = 1.265, P = 0.082). The same tests were made for *Ficus guianensis* fruitfalls (Table 4b) with four of the species tested above (*N. maxima* we had to exclude, because of the low data set). With the chi-squared test only the differences found in *N. pseudolimbipennis* were not significant ($\chi^2 = 8.67$, df = 6, P = 0.193); for the other species they were highly significant (χ^2 = 112, 85, 78.5, df = 6, $P < 0.001$). By using the Kolmogorov–Smirnov test, *N. pseudolimbipennis* was also significantly different at the 5% level (z = 1.39, P = 0.042).

A remarkable temporal change in species abundance was found on one fruit fall of *F. guianensis* (Table 5). Dividing the fruit fall into three equal and successive time periods, in the first time period *N. pseudolimbipennis* was the dominant species with 95.3% of all collected specimens whereas in the two following time periods the assemblage was dominated by *N. glabrata* with 48.5% and 52.3%, respectively. The differences between the first and the two following time periods were highly significant (χ^2 = 96.9, 71.9, df = 4, $P < 0.001$).

The seasonal dependence of *Notiobia* on fig fruits was determined by observing fig fruit fall events throughout the year. Only fruit falls with more than 100 *Notiobia* specimens collected were used for this comparison (n = 25). Less fruit falls occurred in January, February, May, July and November than in the other months (Figure 1). The fruit falls in Figure 1 are assigned to the month in which the main fall occurred. Most started or ended in one of the adjoining months. This indicates that fruit falls in the genus *Ficus* as a whole, are more or less aseasonal.

To determine whether the abundance of individual *Notiobia* species were

Table 4. Differences in abundance of eight *Notiobia* species at the times of different fruit fall events at Reserva Ducke, Amazonia, for (a) one *F. subapiculata* tree (no. 8), and (b) three *F. guianensis* trees.
(a)

	Sep.–Dec. 1992	June–Aug 1993	May 1994	Oct.–Nov 1994	Nov.–Dec 1995
No.	156	41	150	214	361
	%	%	%	%	%
N. pseudolimbipennis	79.5	41.5	70.0	29.9	81.4
N. glabrata	16.0	19.5	18.0	43.9	4.2
N. flavicinctus	3.8		2.7	5.6	3.9
N. nebrioides		26.8	5.3	6.5	6.1
N. umbrifera	0.6			2.8	1.9
N. maxima		7.3	4.0	9.8	2.2
N. aulica		2.4		1.4	0.3
N. disparilis		2.4			

(b)

	Tree no. 1			Tree no. 12			Tree no. 33 May–June 1995
	Aug.–Sep. 1991	Aug.–Sep. 1993	May–June 1995	June–July 1992	Nov.–Dec. 1993	March–Apr. 1995	
No.	83	399	739	23	112	467	171
	%	%	%	%	%	%	%
N. pseudolimbip.	90.4	41.8	75.8	91.3	54.5	61.5	5.8
N. glabrata		40.4	12.9	4.3	4.5	4.5	36.8
N. flavicinctus	3.6	3.3	3.9		29.5	28.1	7.0
N. nebrioides	6.0	7.3	4.3		9.8	5.6	33.9
N. umbrifera			2.7	4.3	0.9		15.2
N. maxima		7.3			0.9		1.2
N. aulica			0.3			0.2	
N. disparilis			0.1			0.2	

Table 5. Differences in abundance of five *Notiobia* species at Reserva Ducke, Amazonia, in three successive time periods during a single fruit fall event of *F. guianensis* tree no. 1 in 1993. Values in parentheses are percentages.

	13 Aug.–30 Aug.	31 Aug.–15 Sept.	16 Sept.–1 Nov.
N. pseudolimbipennis	61 (95.3)	106 (38.7)	44 (22.1)
N. glabrata	3 (4.7)	133 (48.5)	104 (52.3)
N. flavicinctus	0 (0.0)	2 (0.7)	7 (3.5)
N. nebrioides	0 (0.0)	13 (4.7)	29 (14.6)
N. maxima	0 (0.0)	20 (7.3)	15 (7.5)

seasonal or aseasonal we examined the four most common species of this genus (Figure 2). Only one species, *N. flavicinctus*, is possibly seasonal. Six of seven fruit falls, in which this beetle species attained a relative abundance of more than 20%, occurred during the successive months of March, April and May.

The state of gonad maturation for the dissected beetles is summarized in Table 6. Apparently, only two of the seed feeding species, *N. pseudolimbipennis* and *N. flavicinctus*, regularly reproduce on fig fruit falls of the sampled tree species. The percentage of mature females in the other four *Notiobia* species is

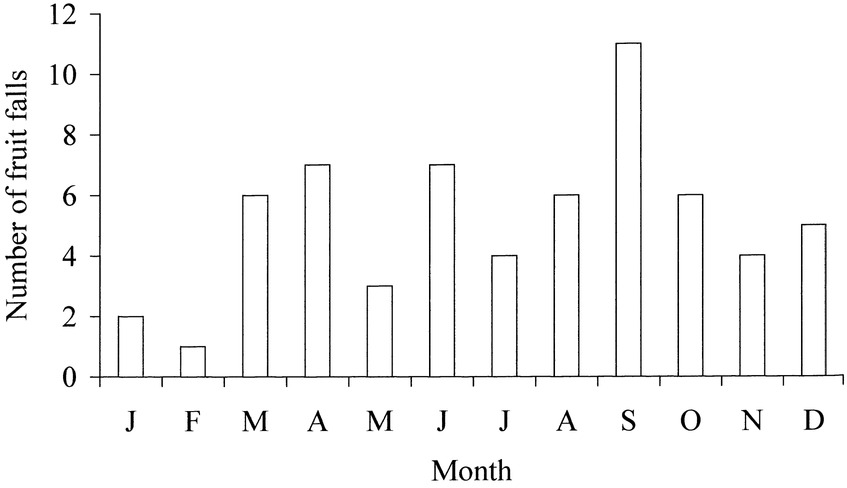

Figure 1. Monthly distribution of the relative abundance of fig fruit fall events at Reserva Ducke, Amazonia, observed throughout the study period of July 1991–August 1996.

very low or zero. More than one third of the individuals representing the most abundant predatory species (*Loxandrus* spec. 1) were mature and 8–11% newly hatched. This indicates that this species also breeds on fig fruit falls. The differences among the percentage of mature males and females is significant (Wilcoxon rank test, z = –2.38, df = 2, P = 0.017).

The sex ratio of the three most common *Notiobia* species was also determined. In *N. pseudolimbipennis* the ratio is quite similar (males 1 : females 1.08, n = 568), while in *N. glabrata* (males 1 : females 0.83, n = 327) and *N. flavicinctus* (males 1 : females 0.7, n = 212), it is male biased.

When fed with fig seeds, 56.8% of the larvae of *N. pseudolimbipennis* (n = 306), 51.7% of *N. flavicinctus* (n = 274), 11.1% of *N. nebrioides* (n = 62) and none of *N. glabrata* (n = 45), *N. umbrifera* (n = 40), *N. maxima* (n = 50) and *N. aulica* (n = 27) developed successfully.

DISCUSSION

Since seed-feeding carabid beetles dominate the large carabid assemblages of fig fruit falls in this study of an Amazonian terra firme rain forest, with 92% of the individuals, it would seem that most carabid beetles in this community are feeding on the seeds themselves. By comparison, the carabid community associated with fig fruit falls in Brunei (Borneo) are dominated by predatory species (62% of the individuals; Borcherding *et al.*, in press). This is also surprising given that there are 42 fig species at the Brunei site (Borcherding & Sapoh, in press) compared with 19 at the Brazilian site (Ribeiro *et al.* 1999). In addition, it is surprising that there are not more seed-feeding carabids at the

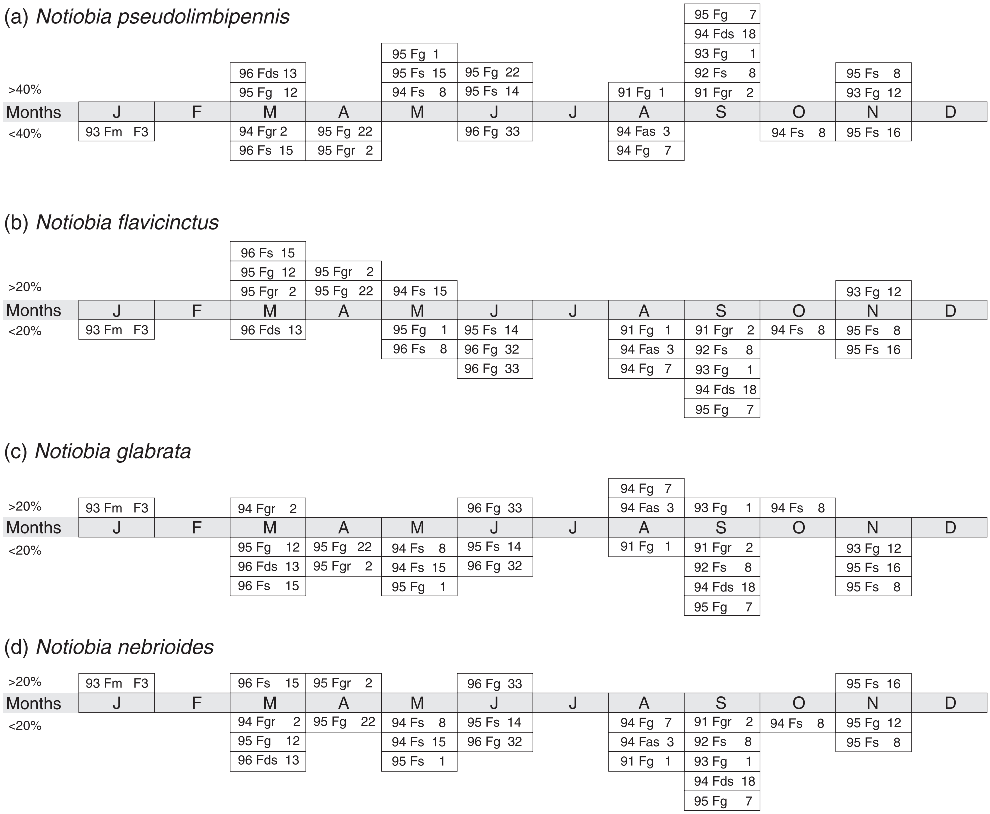

Figure 2. Monthly distribution of the relative abundance of four *Notiobia* species (above or below a certain level: 40% for *Notiobia pseudolimbipennis*, 20% for *N. flavicinctus*, *N. glabrata* and *N. nebrioides*) at fig fruit falls at Reserva Ducke, Amazonia. Data only included for those fig fruit falls (n = 40) where more than 100 *Notiobia* beetles were collected. Symbols in boxes: (1) year of observation, (2) abbreviation for fig species (see Table 1), and (3) number of individual fig trees (out of 40).

Brunei site since the number of fruit falls per unit area is higher than in Brazil (R. Borcherding & W. Paarmann, unpubl. data). This may be explained by the fact that at the Brazil site in 28 of 29 fruit falls of different fig species the fruits contain numerous small seeds (Gutzmann 1995, Küppers 1995, Niers 1994, Stumpe 1997) whereas the number of seeds in Bruneian fig fruits is low in most cases and the seeds are usually much larger (Borcherding *et al.*, in press). About half of the Brunei fig species with high seed production have seeds that are too large to be opened by larvae and adult beetles. However, predatory species can feed on other insect larvae and adults, particularly Diptera, that use the fig fruit falls and large piles of fallen leaves that occur on the ground in Brunei. Such accumulations of leaves did not occur at the Brazilian site.

From the results of the dissections and the breeding experiments we conclude that only two of the eight *Notiobia* species are fig seed specialists. These

Table 6. Proportions (%) of mature and immature specimens of eight *Notiobia* species and one *Loxandrus* species as well as the proportion of teneral and parasitized specimens of all dissected beetles from *Ficus* fruit falls at Reserva Ducke, Amazonia.

	Stages				
	% mature	% immature	% teneral of total	% parasitized of total	n
Males					
N. pseudolimbipennis	73.3	26.7	8.0	1.5	273
N. flavicinctus	84.0	16.0	1.6	2.4	125
N. glabrata	22.0	78.0	1.0	0.0	179
N. nebrioides	13.0	87.0	2.9	0.0	69
N. maxima	21.4	78.6	3.6	0.0	28
N. umbrifera	10.0	90.0	0.0	0.0	20
N. aulica	11.8	88.2	0.0	0.0	17
Loxandrus spec. 1	62.0	28.0	10.0	0.0	50
Females					
N. pseudolimbipennis	59.7	40.3	12.9	0.7	295
N. flavicinctus	62.1	37.9	2.3	0.0	87
N. glabrata	4.1	95.9	2.7	0.0	148
N. nebrioides	0.0	100.0	0.0	0.0	70
N. maxima	0.0	100.0	0.0	0.0	13
N. umbrifera	4.8	95.2	4.8	0.0	21
N. aulica	15.4	84.6	0.0	0.0	13
N. disparilis	0.0	100.0	0.0	0.0	4
Loxandrus spec. 1	38.9	61.1	8.3	0.0	36

species, *N. pseudolimbipennis* and *N. flavicinctus,* cope with the problem of a comparably short fruit fall duration by finding new fruit falls quickly, rapidly establishing populations (Tables 5 and 6), and adults reaching full maturity in a short time. At the beginning of a fruit fall most females have reduced ovaries, but in some cases they carry a few (1–4) fully developed eggs, called 'transport' eggs in their oviducts or the uterus. Such 'transport' eggs were also observed in females of fruit-fall-dwelling Carabidae in Brunei rain forest (Borcherding *et al.*, in press). 'Transport' eggs are deposited immediately on arrival at a new fruit fall. The female then needs *c.* 1 wk to develop new eggs. The later the larvae hatch during the course of the fruit fall, the greater their chance of facing a food shortage at the end of a fall. Most seeds disappear very quickly, either because they are eaten by other animals, such as termites (Holzkamp 1998) and mammals (Stanke 1992, Whitmore 1993), or they germinate (W. Paarmann, *pers. obs.*). When this seed shortage occurs, the larvae change from being seed feeding to becoming predatory or cannibalistic with large larvae killing and feeding on the smaller ones (Vanicek 1993, Vanicek *et al.* 1994). Newly hatched adult beetles (teneral) have to migrate from the leached fruit fall site to find a new food source.

The two fig seed specialists are of different size (Arndt 1998) and are sympatric on fruit falls. *Notiobia flavicinctus* is usually less abundant and only about half of the size of the larger species *Notiobia pseudolimbipennis*. When food is in short supply, the smaller species may be at an advantage, because fewer seeds are needed for this species to reach full gonad maturation and for larvae to complete their development. On the other hand, the first instar larva of *N. flavic inctus* may have more difficulty in opening seeds than those of *N. pseudolimbipennis* because of its smaller mandibles. Also the third larval instar of *N. flavicinctus* may face problems because of its small size at the end of a fruit fall when seeds are in short supply and the larvae are forced to become predators. These problems will be investigated in the future.

While the sex ratio in *N. pseudolimbipennis* is nearly equal, in *N. flavicinctus* it is distinctly male biased. This may be explained by a significantly longer life span in males than in females as observed in our laboratory cultures (W. Paarmann, *pers. obs.*).

Competition does not seem to occur among the adults. During most of the time a fruit fall lasted, its full capacity was not attained (Paarmann *et al.*, in press). Adults avoid competition at the end of the fruit fall by leaving the site.

The remaining six species of *Notiobia* do not appear to reproduce on fig fruit falls (Table 6). Four species (*N. aulica*, *N. glabrata*, *N. maxima*, *N. umbrata*) have host trees in Melastomataceae (genera *Bellucia*, *Loreya* and *Miconia*) (W. Paarmann *et al.*, unpubl. data) and *N. nebrioides* has host tree species in Clusiaceae (genus *Vismia*) and Cecropiaceae (genus *Coussapoa*) (W. Paarmann *et al.*, unpubl. data). The host tree species of *N. dispar* (only four individuals were collected) is still unknown. These six *Notiobia* species use the fig fruit falls as 'stepping stones' during their migration between fruit falls of their individual host trees, which can be separated by large spatial and temporal distances. Fruit production in Melastomataceae is particularly seasonal (Renner 1984, 1989).

The dominance structure of the spermatophagous carabid guild on fig fruit falls seems to be very stable, based on 5-y data in this study (Table 3), although there is high variability between individual fruit falls (Table 4). The aseasonal fruiting of figs is explained by their pollination biology (Boucek 1993, Whitmore 1993, Wiebes 1986). The variation in abundance of the fig seed specialists may have multiple causes including variation in fruit fall abundance and fruit fall quality and/or the possible use of aggregation pheromones in combination with fruit fall quality.

The abundance of the non-fig seed specialists appears to depend on the seasonal fluctuations of their host tree fruit falls and possibly on a low migration range. When the fruit fall of a host tree comes to an end adults need to migrate only to the nearest fig fruit fall, thus causing a sudden increased assemblage on this fruit fall.

Which mechanisms maintain the diversity of the seed feeding ground beetle guild of the genus *Notiobia*? On the one hand they are specialized on certain seeds as food for a successful larval development (deterministic process) and yet the non-fig seed specialists consume fig seeds in order to survive periods of food shortage. The necessity to do so limits the tendency to specialize. If stochastic processes do play a role in maintaining the diversity of the seed-feeding

Notiobia species, they are probably less important than deterministic processes. These species may be viewed as 'chance specialists' adapted to the unpredictability of fruit falls. The fig seed specialists can be included in the 'touring company' described by Leighton & Leighton (1983) for birds and mammals. These animals move from one fig fruit fall to the next and therefore depend on there being a sufficient occurrence and density of such fruit falls throughout the year.

The diversity of the non-fig seed specialists is based on the diversity of their own host tree species of the family Melastomataceae or the families Cecropiaceae and Clusiaceae (W. Paarmann *et al.*, unpubl. data) but use fig fruit falls during periods of food shortage as fig fruit falls are available throughout the year. It would appear from this study that *Ficus* is as much a keystone resource for some ground beetle species, as it is for many other animals of tropical rain forest (Terborgh 1986).

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