

VARIATION IN TERMITE ALATE SWARMING IN RAIN FORESTS OF CENTRAL AMAZONIA

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Resumo. As revoadas de alados (= formas reprodutivas) de cupins numa floresta de terra firme da Amazônia Central (Reserva Florestal Adolpho Ducke) foram estudadas com 2 armadilhas luminosas em coletas bi-semanais que funcionaram continuamente durante 2 anos (176 intervalos de coleta). Aqui apresentamos os dados sobre a variação de eventos de revoadas nas famílias de térmitas, em tempo e espaço. Térmitas foram presentes em 64-83% de todas as coletas, e não havia um mês sem revoadas. Um total de 25.500 cupins de três famílias foi coletado. A família Termitidae rendeu 91-98% do número de indivíduos registrados por armadilha e ano, 2-8% foram Kalotermitidae, e 0.5-2% Rhinotermitidae. O tamanho médio da coleta por armadilha e mês foi de 3.8 indivíduos em Rhinotermitidae, 38.4 em Kalotermitidae, e 467.3 em Termitidae; máximas das coletas foram 20, 490, e 5940 indivíduos por armadilha e mês, respectivamente. Porém, a frequência de revoadas de Termitidae (45-55% dos intervalos de coleta) não foi maior que a de Kalotermitidae (41-58%); a frequência de Rhinotermitidae foi baixa (8-18%). Para avaliar a variação de eventos de revoada com o tempo, nós testamos por correlação entre os eventos de revoada (número total de indivíduos, número total em cada família, frequência por família e presença/ausência em cada família) das 2 armadilhas e dos anos. Nenhuma correlação foi encontrada. A distância entre ambas armadilhas foi de apenas ≈ 500m, mas os números totais de coleta anual variaram consideravelmente entre elas, o que indica grandes variações das revoadas em pequena escala (armadilha I/II: 7.500/2.600 indivíduos no período de 91-92; 4.500/9.700 em 92-93). Também apenas 18, 32 e 36% das revoadas de Rhinotermitidae, Termitidae e Kalotermitidae, respectivamente, ocorreram simultaneamente em ambas as armadilhas. Como revoadas de térmitas variam consideravelmente em tempo, tamanho e extensão, levantamos a hipótese de que a colonização de um determinado lugar na floresta por uma determinada espécie de cupim é altamente imprevisível, o que poderia explicar a distribuição em forma de mosaico dos cupins, e o alto endemismo de térmitas encontrado em diferentes áreas da Amazônia.

Abstract. The swarming of termite alates (= reproductive forms) in a Central Amazonian terra firme rain forest (Reserva Florestal Adolpho Ducke) was studied with 2 light traps which were emptied twice per week and continuously run for 2 years (176 sampling intervals). Here, we present the data on variation of swarming events in the termite families, in time and space. Termites were present in 64-83% of all catches, and there was no month without swarming. A total of 25,500 termites of three families was collected. The family Termitidae accounted for 91-98% of the number of individuals recorded per trap and year, 2-8% were Kalotermitidae, and 0.5-2% Rhinotermitidae. Average catch size per trap and month was 3.8 individuals in Rhinotermitidae, 38.4 in Kalotermitidae, and 467.3 in Termitidae; maximum catches were 20, 490, and 5940 individuals per trap and month, respectively. However, the swarming frequency of Termitidae (45-55% of the sampling intervals) was not higher than that of Kalotermitidae (41-58%); the frequency of Rhinotermitidae was low (8-18%). To assess the variation of swarming events with time, we tested for correlation between the swarming events (total individual numbers, total numbers for each family, frequency per family and presence/absence for each family) of the 2 traps and of the 2 years. No correlations could be found. Both traps were only ≈ 500 m apart, but the total annual catch numbers varied considerably between them, which points to large small-scale variation in swarming (Trap I/II: 7,500/2,600 individuals in the 91-92 period; 4,500/9,700 in 92-93). Also, only 18, 32 and 36% of the Rhinotermitidae, Termitidae and Kalotermitidae swarms, respectively, occurred simultaneously in both traps. As termite swarms vary considerably in timing, size and extension, we hypothesize that the colonization of a determined spot of forest by a particular termite species is highly unpredictable, which could explain the patchy distribution of termites and the high endemism of termites found in different parts of Amazonia. Accepted 24 February 1996.

Key words: Amazonia, rain forest, Isoptera, termite families, dispersion.

INTRODUCTION

Termites are social insects; a termite colony can be seen as a sessile "superorganism" (Moritz & Southwick 1992) consisting of a reproductive "royal" pair, and sterile workers and soldiers which forage in the vicinity of the nest. Dispersal is generally accomplished by winged, sexually mature imagoes (alates) which are produced in certain stages of the life cycle of a colony (Noirot 1969). Alates must leave the nest and swarm in order to induce mating behaviour (Messerli & Di Battista 1992), and swarming must be synchronized between the colonies of a species to allow outcrossing between them. The basic sequence of the reproductive process - swarming, mating and colony foundation (Stuart 1969, Nutting 1969) - guarantees both sexual reproduction and spatial dispersion. How successful is dispersion? The dispersal power depends on various factors: Number of alates released per swarming event, number of swarms released per year or colony lifetime, flight duration and range, adaptive value of triggers which release swarming, susceptibility to predation and presence of predators, etc.

About 90 termite species are found on a single hectare of rain forest in Amazonia (Bandeira 1978, Bandeira 1989, Apolinário 1993, Souza 1989, Souza & Brown 1994, Martius 1994). Species appear to be distributed in a "mosaic" (Apolinário 1993; Souza & Brown 1994; Marrius 1989, and unpubl.), but the reasons for this pattern are not apparent. Is termite species distribution in a given patch of forest totally predetermined by the biotic and abiotic requirements of the species or is it more influenced by stochastic processes at the moment of swarming?

A high endemism is also observed in Amazonian termite species. Only a few species have a wide distribution, and termite assemblages show large regional differences in species composition. Constantino (1992) found that only 5 out of 100 identified species occurred at any of 8 different sites investigated. Could this be explained by the dispersal power of the termite species?

We studied termite alate flight patterns in a Central Amazonian rain forest with two light traps which were continuously run from September 1991 to September 1993. In this paper we present basic descriptive data and analyze synchronicity and correlation of swarming patterns in time and space by comparison of the catches from both years and both traps. In forthcoming publications we will

consider the correlation of flight with abiotic parameters and analyze the data on the level of genera and species.

If the distribution of the colonies of a termite species is mainly determined by its response to abiotic factors, swarming patterns and flight range of the alates of this species should be such that every spot of forest has an equal probability of being reached by the alates. Such a species should either be abundant or have a high dispersal power, or both. On the contrary, dispersion of rare species with weak dispersal power should be determined mainly by stochastic processes effective at the time of swarming, and the outcome should be a highly unpredictable distribution pattern. Although the prevailing process may differ from species to species, we ask here whether a dominant pattern is recognizable in the swarming of the termite families. If the majority of the species consists of strong dispersers, swarming events should be highly correlated between the traps. If most species disperse weakly, correlation between the traps should be low. Additionally, we used testing for autocorrelation of time series to investigate whether swarming patterns repeat from year to year.

MATERIAL AND METHODS

The Brazilian federal forest reserve "Reserva Florestal Adolpho Ducke" is a quadrat of 10 x 10 km of undisturbed forest north of the city of Manaus, in central Amazonia (2°55'S, 59°59'W). Details on soil (predominantly latossol) and vegetation (a primary undisturbed rain forest) are given in Gentry (1990); general information on climate can be found in Ribeiro (1976). The total annual precipitation was 1790.9 mm in the first year (October 1991 to September 1992), and 2166.4 mm in the second year of the study (October 1992 to September 1993). Average annual temperature was 26.4° and 25.3°C in the first and in the second year, respectively. (The climate data from the meteorological station at Reserva Ducke, situated at a distance of about 1 km from the traps, were supplied by the Department of Meteorology of INPA.)

Two light traps (labelled RD-I and RD-II) type "Walz" (Mühlenberg 1989; manufactured by Ecotech, Bonn, Germany), equipped with normal fluorescent light sources, were operated for 25 months (11 September 1991 to 28 September 1993) at a distance of about 0.5 km of each other in a primary forest site on a plateau in the reserve. The traps were suspended at a height of 3 m above the ground. They were operated

with car batteries which were exchanged twice a week and charged in the laboratory. An automatic switch coupled to a foto-sensitive element turned the traps on approximately 0.5 hour before sunset and switched them off after sunrise. Technical details are given in Rebello & Martius (1994), however, we improved the arrangement by using solar panels which were set up on trees at a height of about 10 m. The panels provided enough additional power to allow uninterrupted operation of the traps between the sampling visits. This considerably reduced the occurrence of sampling interruptions in comparison to the study of Rebello & Martius (1994). The collecting vials of the traps were equipped with a 10% solution of formol. They were emptied twice a week. All collected insects were transferred into alcohol 70% and sorted to order. Here we report on termites only which were sorted to families. Three families of Isoptera occur in the Amazon region: Kalotermitidae, Rhinotermitidae, and Termitidae.

Trap efficiency. Ideally, regular collection of two samples per week is accomplished with alternating sample intervals of 3 and 4 days. Technical problems led to occasional disruptions of the sampling rhythm and real sample intervals varied from 1 to 8 days (average ± S.D. = 3.53 ± 0.77 days). The total sample period of 25 months was split up into 214 single sample intervals.

A month has, potentially, 5-10 sample intervals (NTP in Table 2; average 8.56 ± 0.98); however, only 3-9 intervals per month were actually sampled (NTC in Table 2; average 7.04 ± 1.61). We joined 105 sample intervals to form a year (October to September; the first 4 intervals in September 1991 were eliminated); only 92 and 80 intervals were actually sampled in 1991-92 and 1992-93, respectively (88 and 77%). *Data analysis.* The relative abundance (A) of a family in the catches is:

$$A = \frac{NIF}{NIT} \tag{1}$$

with NIF = number of individuals per family, trap and year; NIT total number of individuals collected per trap and year (Table 1).

In order to analyze swarming phenology independently of factors related to density and distribution, the relative frequency (F) of the termite alates (total and families) was calculated as follows:

$$F = \frac{NCA}{NIT} \tag{2}$$

with NCA = number of sample intervals per month or per year and trap in which alates of a given family

TABLE 1. Individual numbers and relative abundance A (cf. formula 1) of termite alates in light traps in 1991-1993 in a primary rain forest of the Reserva Ducke, Central Amazonia. K = Kalotermitidae, R = Rhinotermitidae, T = Termitidae. RD-I = trap I, RD-II = trap II.

Families ▶	RD-I			RD-II			both traps (RD-I + RD-II)			RD-I	RD-II	both traps
	K	R	T	K	R	T	K	R	T	Total	Total	Total
Individual numbers												
91-92*)	307	51	7090	178	57	2412	485	108	9502	7448	2647	10095
92-93*)	378	28	4127	189	51	9428	567	79	13555	4533	9668	14201
Total	1065	79	11502	854	110	11864	1919	189	23366	12646	12828	25474
Relative abundance												
	Per Cent (Total RD-I = 100 %)			Per Cent (Total RD-II = 100 %)			Per Cent (both = 100			Per Cent (both = 100 %		
91-92*)	4.1	0.7	95.2	6.7	2.2	91.1	4.8	1.1	94.1	73.8	26.2	
92-93*)	8.3	0.6	91.0	2.0	0.5	97.5	4.0	0.6	95.5	31.9	68.1	
Total	8.4	0.6	91.2	6.7	0.9	92.5	7.5	0.7	91.7	49.6	50.4	

*) October to September

were present; NTC = total number of sample intervals or "catches" per month or year and trap (Tables 1, 3). As >1 family can occur in one interval, the sum of the F's of the 3 families may exceed 1.0 (Tables 2, 3). Rebello & Martius (1994) related the NCA's of the families to total NCA, instead of NTC, and in the present paper the family values taken from this source have been recalculated for comparison.

RESULTS

Individual numbers. A total number of 25,474 alates was captured in both light traps in 25 months; total numbers from the 2-year period are almost equally distributed between the traps (12,646 and 12,828 individuals in trap I and II, respectively), but a 41% higher total catch was recorded in the second year (10,095 individuals in 91-92, 14,201 individuals in 92-93). Total catches for single traps and years are irregularly distributed: In 91-92, trap I contributed with 74% of the total catch of this year, but in 92-93 it was trap II, with 68% of the total catch, which contributed more (Table 1).

The family Termitidae contributed most to individual numbers (relative abundance $A = 91-98\%$ of the total catches per year and trap; average 91.7% for traps and years pooled). The next numerous family was Kalotermitidae, which contributed 2-8% of the total individual numbers per trap and year (average 7.5%). Rhinotermitidae generally contributed less than 1% (range 0.5-2%, average 0.7%) (Table 1).

The average number of individuals per trap and sampling interval is 66.0 in Termitidae, 5.5 in Kalotermitidae, and 0.5 in Rhinotermitidae. If average numbers are pooled to month, they amount to 467.3, 38.4, and 3.8 individuals per trap and month, respectively. In Kalotermitidae and Rhinotermitidae, monthly catches never surpass 500 individuals, whereas 18% of the monthly Termitidae catches consisted of >500 individuals. In Termitidae, maxima of up to 3190 individuals per trap and sample interval were recorded. Kalotermitidae and Rhinotermitidae catch maxima were much lower, at 410 and 20 individuals per trap and sample interval, respectively. There is no correlation between the length of the sampling intervals and the number of individuals captured. If total catches are pooled to month, they amount to 5940 individuals per trap and month in Termitidae, 490 in Kalotermitidae and 30 in Rhinotermitidae.

The relative importances of alate individuals of the 3 families in the light traps thus differ by one to two

orders of magnitude. In contrast, the differences between catches per month and catches per sample interval are almost negligible in terms of order of magnitude. This indicates that termite swarms are extremely short-termed events; the sum of alates collected in a month is much more characterized by single large swarms than by a continuous trickle of alates in low numbers during that period. Nevertheless, termite flights are frequent, as termite alates were present in 64-83% of the samples per year and trap (Table 2). With the exception of May 1993 in trap I, there was no month without termite flight. Other major gaps in swarming activity (e.g., March and May to June 1993) correspond to major sampling interruptions due to technical problems (months in which >30% of the sample intervals are missing; Table 2).

Frequencies. We used the monthly relative frequencies to assess swarming phenology independently of the number of individuals captured because the latter depends on density (Termitidae colonies are often more populous than those of the other families) and distribution (Termitidae colonies are more frequently found, which makes it more likely that a Termitidae colony is within the area of influence of the light trap). The relative frequency expresses the number of sampling intervals in which alates were recorded as percentage of the total number of sample intervals in which traps were run. The frequency of Termitidae is much lower than suggested by the individual numbers in this family; it varies between 45 and 55% per trap and month (Table 3), which is within the range of the frequency of Kalotermitidae (41-58%). Rhinotermitidae, which represent only 0.7% of the individual numbers, were present in 8-18% of the catches. Several times Kalotermitidae and Termitidae were present in 70-100% of the monthly catches, whereas Rhinotermitidae reached 50% only in one month (May 1992; Table 3).

Variation in space and time. The frequencies of total alates and of the families in trap I were higher than in trap II (Tables 2,3), although not statistically significant. As missing sample intervals occurred always simultaneously in both traps, the differences in frequencies can be no artifact and indicate a difference of swarming intensity between the sites.

In order to view the synchronicity of the catches in both traps we plotted presence (value = 1) or absence (value = 0) of termite families in the sample intervals against time (Fig. 1). In only 18-36% of the 176 catch intervals in the two-year period, depending on

the family, swarming occurred simultaneously in both traps (Table 4). The lowest synchronicity was found in Rhinotermitidae (18%), and 32-36% of all flight events in Termitidae and Kalotermitidae were synchronous.

We used a non-parametric test for analysing the correlation between the catches in the traps (Spearman rank order correlation). We tested total individual number of termites per trap and individual number per family and trap (both years together) and found no correlation between the traps for the individual num-

bers (Appendix). Similarly, we tested the correlation with the presence/absence data set underlying Figure 1 and with the relative frequencies, and found no correlation. We then separated the annual catches (individual numbers) and tested again for correlation of the catches from both traps. Here also, no correlations could be found. Finally, we unsuccessfully tested individual numbers for correlation from one year to the other (autocorrelation of time series). In all these cases, correlation coefficients are much too low to assume the existence of a statistical correlation (Appendix).

TABLE 2. Number of monthly sample intervals, trap efficiency (proportion of missing sample intervals due mainly to technical problems) and flight frequencies of termite alates (total Isoptera) in a rain forest, Reserva Ducke, Central Amazonia. Total ("potential") number of sample intervals per month (NTP), total number of sample intervals in which traps were active (NTC), percent of missing sample intervals, monthly number of sample intervals in which termites were present (NCA), and monthly relative frequencies (NCA/NTC).

Months	Total of Intervals (NTP)	NTC	Missing sample intervals (NTP-NTC/NTP · 100)	NCA				Frequencies	
				(%)	RD-I	RD-II	RD-I	RD-II	
91-93									
S	5	4	20	4	4	1.00	1.00		
O	9	9	0	8	6	0.89	0.67		
N	8	8	0	8	6	1.00	0.75		
D	9	9	0	9	6	1.00	0.67		
J	9	8	11	8	5	1.00	0.63		
F	8	6	25	6	5	1.00	0.83		
M	8	7	13	6	2	0.86	0.29		
A	9	8	11	7	2	0.88	0.25		
M	8	8	0	6	7	0.75	0.88		
J	9	8	11	3	7	0.38	0.88		
J	9	5	44	5	4	1.00	0.80		
A	10	7	30	3	5	0.43	0.71		
S	9	9	0	7	4	0.78	0.44		
O	8	8	0	5	6	0.63	0.75		
N	9	9	0	7	7	0.78	0.78		
D	9	6	33	3	4	0.50	0.67		
J	8	8	0	6	7	0.75	0.88		
F	9	7	22	3	6	0.43	0.86		
M	10	5	50	5	1	1.00	0.20		
A	9	6	33	4	5	0.67	0.83		
M	9	3	67	0	2	0.00	0.67		
J	7	5	29	4	1	0.80	0.20		
J	9	8	11	6	7	0.75	0.88		
A	9	7	22	7	6	1.00	0.86		
S	8	8	0	5	6	0.63	0.75		
Total	214	176	18	135	121	0.77	0.69		
91-92*	105	92	12	76	59	0.83	0.64		
92-93*	105	80	23	55	58	0.69	0.73		

*) October to September

TABLE 3. Relative Frequencies of termite alate families in light traps in 1991–1993 in a primary rain forest of the Reserva Ducke, Central Amazonia. Number of sample intervals per month in which termites belonging to one family were recorded (NCF), and frequencies (NCF/NTC · 100). K = Kalotermitidae, R = Rhinotermitidae, T = Termitidae. RD-I = trap I, RD-II = trap II.

Months	NCF						Frequencies					
	RD-I		RD-II			RD-I		RD-II				
	K	R	T	K	R	T	K	R	T	K	R	T
S	3	0	3	4	1	2	0.75	0.00	0.75	1.00	0.25	0.50
O	8	2	5	4	1	4	0.89	0.22	0.56	0.44	0.11	0.44
N	7	1	2	6	1	2	0.88	0.13	0.25	0.75	0.13	0.25
D	8	1	5	6	2	5	0.89	0.11	0.56	0.67	0.22	0.56
J	4	0	7	5	3	5	0.50	0.00	0.88	0.63	0.38	0.63
F	3	1	5	2	1	4	0.50	0.17	0.83	0.33	0.17	0.67
M	2	0	5	0	1	2	0.29	0.00	0.71	0.00	0.14	0.29
A	5	3	6	0	1	1	0.63	0.38	0.75	0.00	0.13	0.13
M	4	4	5	3	3	6	0.50	0.50	0.63	0.38	0.38	0.75
J	1	2	2	3	2	5	0.13	0.25	0.25	0.38	0.25	0.63
J	4	1	2	4	1	1	0.80	0.20	0.40	0.80	0.20	0.20
A	2	1	1	4	1	4	0.29	0.14	0.14	0.57	0.14	0.57
S	5	0	6	1	0	2	0.56	0.00	0.67	0.11	0.00	0.22
O	5	0	4	6	0	3	0.63	0.00	0.50	0.75	0.00	0.38
N	5	1	5	5	1	5	0.56	0.11	0.56	0.56	0.11	0.56
D	3	0	2	2	1	2	0.50	0.00	0.33	0.33	0.17	0.33
J	0	1	6	3	3	7	0.00	0.13	0.75	0.38	0.38	0.88
F	1	1	3	1	2	5	0.14	0.14	0.43	0.14	0.29	0.71
M	1	1	5	0	0	2	0.20	0.20	1.00	0.00	0.00	0.40
A	3	0	2	2	1	3	0.50	0.00	0.33	0.33	0.17	0.50
M	0	0	0	1	0	1	0.00	0.00	0.00	0.33	0.00	0.33
J	3	0	2	1	0	0	0.60	0.00	0.40	0.20	0.00	0.00
J	6	1	2	4	1	2	0.75	0.13	0.25	0.50	0.13	0.25
A	6	1	5	5	1	2	0.86	0.14	0.71	0.71	0.14	0.29
S	5	0	4	6	0	4	0.63	0.00	0.50	0.75	0.00	0.50
Total	94	22	94	78	28	79	0.53	0.13	0.53	0.44	0.16	0.45
91-92*	53	16	51	38	17	41	0.58	0.17	0.55	0.41	0.18	0.45
92-93*	38	6	40	36	10	36	0.48	0.08	0.50	0.45	0.13	0.45

*) October to September

DISCUSSION

Relative importance of termite families. The high relative abundance of the Termitidae in the light traps reflects the importance of this family in termite assemblages which to about 80% consist of species of this family (Martius 1994). Rhinotermitidae account for 3-20% of the termite communities, and their alates are both low in relative abundance and frequency in the light traps. Dry-wood termites (Kalotermitidae) however, have been registered to diverging extent in previous termite population assessments. In many studies, they have not been found, in others, they

contribute 2-12% to the total number of species (Bandeira 1979, 1983, 1989, Souza 1989). This corresponds to the relative abundance of the alates of this family in the light traps of the present study (2-8%). Rebello & Martius (1994) stated that Kalotermitidae must be important elements of termite assemblages in floodplains where this family had not been registered in assessments prior to the flight trap catches. Here, we can assess that although only 5 species of Kalotermitidae have been recorded in non-flooded terra firme rain forest in Central Amazonia (Apolinário 1993), their swarms represent an important proportion of all swarming events (Kalo-

termitidae living in the canopy, which might add to the species number, have never been assessed). Although a much lower number of Kalotermitidae than of Termitidae individuals has been caught in the traps, both families are equal in frequency. A probable explanation is that a single colony of a Kalotermitidae species can release more swarms per season than a Termitidae colony.

Swarming seasonality. Former light trap catches in Amazonian floodplain and secondary forests had shown that swarming of termites occurs almost continuously throughout the year (Rebello & Martius 1994). The present study confirms this result for primary terra firme forest. Although termites were recorded in only 64-83% of the sample intervals (Table 2), there was, with the exception of May 1993 (trap 1), no month without termite flight when total catches are considered.

These results contrast with findings in other, sub-tropical arid and semi-arid regions of the earth (e.g., Bednarzik 1983, Akhtar & Amanullah 1989, Akhtar & Shahid 1990, Kumar & Thakur 1990, Clarke 1993), where termite swarming is confined to a narrow

time window, often related to the rainy season. The prolonged rainy season in the humid tropics (there is only a weak seasonality in rainfall distribution over the year in Central Amazonia) allows an extension of the swarming period and could therefore permit the existence of an elevated diversity of termites in the permanent humid tropics.

Year-to-year correlation of swarms. Large year-to-year differences in catches of flying insects have been reported from long term studies in Panama (Wolda 1978, 1992) and also from our previous study of alate swarming in a floodplain forest (Rebello & Martius 1994). In the latter study, one single swarm of Rhinotermitidae in one year of the study inverted the relative importance of the families in this year.

In the present study, we detected no correlation between the catches of the different years. Termite flight is triggered by external climatic factors (e.g., rainfall or variation in atmospheric pressure; Nutting 1969), events which are seasonal but occur following a chaotic or stochastic pattern. Thus, it could be expected that annual time series of swarming events would not be correlated. The second year was characterized by

TABLE 4. Synchronicity of termite catches in two traps in a primary forest, Reserve Ducke, Central Amazonia, 1991-1993.

	RD-I only	RD-II only	(RD-I + RD-II) simultaneously	Catch events without termites	Total
<i>Kalotermitidae</i>					
No. of sample intervals with termites	49	32	45	50	176
Sum (= 100%)	126				
Per Cent	38.9	25.4	35.7		
<i>Rhinotermitidae</i>					
No. of sample intervals with termites	14	22	8	132	176
Sum (= 100%)	44				
Per Cent	31.8	50.0	18.2		
<i>Termitidae</i>					
No. of sample intervals with termites	52	39	42	43	176
Sum (= 100%)	133				
Per Cent	39.1	29.3	31.6		

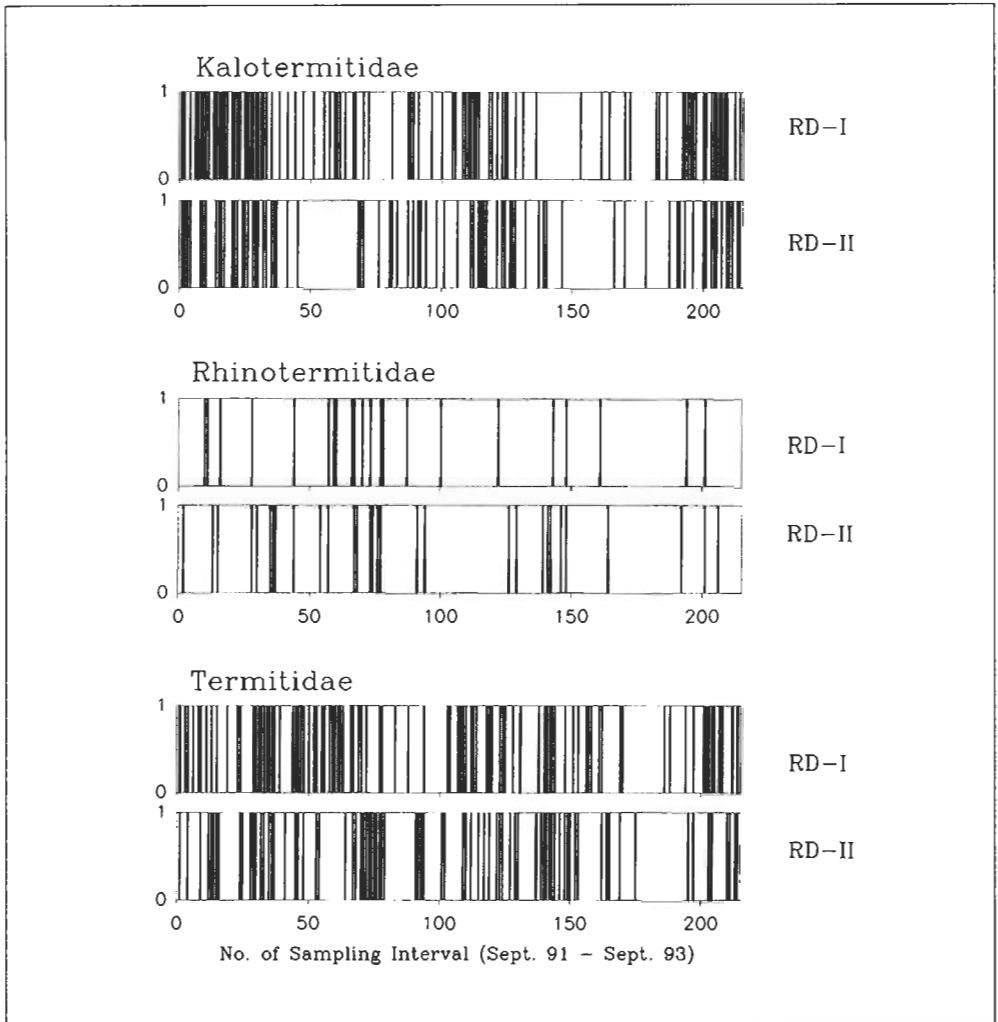


FIG. 1. Occurrence of alate swarming in the three termite families in two light traps (RD-I and RD-II) in a primary rain forest, Reserva Ducke, Central Amazonia. X-axis = time; numbers indicate sample intervals from September 1991 to September 1993.

a total precipitation about 21% higher than that of the first year (though the difference is not statistically significant; *t*-Test), and the average annual temperature was 4% lower (statistically significant; Mann-Whitney rank sum test; $P < 0.001$) (see Material and Methods). It is, however, very unlikely that the changes in total annual rainfall or average annual temperature influenced the catches, as the total catch number increased in trap RD-II and decreased in trap RD-I, and the

variations in the catches of the families show no clear trend (Table 1).

Variation in space. The differences of swarming events in the two light traps which were only 500 meters apart are intriguing. Total annual catches differ strongly (Table 1), frequencies of the families between the two traps are not correlated, and synchronicity is very low (Fig. 1; Table 4). With the traps set at such a small distance in parts of the forest which seemingly are of

homogenous structure, we expected that most swarms should be recorded simultaneously in both traps, but this happened to occur in only 18-36% of the catch events, and the majority of the catches in the two traps was not synchronous. This indicates that swarming alates do not uniformly browse the forest for mates and nesting sites, but that the range of most swarms is rather limited. We hypothesize that, in this sense, most termites species must be weak dispersers, whose dispersal is much more subject to stochastic processes (p.ex. distribution of existing colonies) than to the biotic and abiotic factors which determine the carrying capacity of the environment (e.g., predator density, soil factors, availability of food).

However, many catches consist of more than one species, some of which may have larger flight ranges and higher synchronicity of the flight than the average. Ultimately, only the forthcoming analysis on the species level will allow to understand flight dispersal patterns. Nonetheless, if further studies confirm that most species swarm at low distances and ranges only, two consequences arise: First, colony foundation is more likely to be successful in the vicinity of existing nests, perpetuating the existing mosaic distribution of termite colonies. Second, inbreeding must be high, in which case dispersal by "budding" might be favoured by evolution over swarming. Budding, which is the appearance of filial nests which can separate from the parental nest and become independent colonies, represents a strategy of short-distance dispersal which does not allow for sexual reproduction, but it might be favoured as a dispersal strategy which is much less risky than swarming (during which generally >90% of the alates are killed; Wood & Sands 1978, Lepage 1991). Both small-scale swarming and budding result in a strong patchy distribution.

Distribution of weak dispersers on a larger scale would then be restrained to rare opportunities, e.g., when strong wind currents during storms carry alates over longer distances. Such a dispersal constraint (low dispersal power, small-scale dispersion favoured) would account for the high endemism observed in termites throughout Amazonia and explain why so few species are widely distributed.

CONCLUSIONS

Termitidae account for >90% of the alates recorded in light traps in terra firme rain forest of Central Amazonia, but the frequency of flight events is equally high for Termitidae and Kalotermitidae (swarms of

both families are found in 41-58% of the sample intervals per month). Rhinotermitidae numbers and frequencies are much lower.

Swarming occurs almost uninterruptedly throughout the year. Swarming shows no reproducible pattern from year to year (no autocorrelation of annual time series can be observed).

Swarming events as recorded by two neighbouring traps are not correlated; total annual catches (individual numbers) differ by about 70% between the traps, and only 18-35% of the family catches occur simultaneously. This indicates a probable low dispersal power of most of the termite species which would explain the patchy mosaic of species distribution and account for the high endemism found in this taxon throughout Amazonia.

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APPENDIX

Light trap catches of termite alates in a primary rain forest, Reserva Ducke, Central Amazonia. Results of the tests for correlation between traps and years (Spearman rank order correlation). Only data sets with correlation coefficients nearing 1.0 and P values <0.05 would be positively correlated.

	Total	Kalotermitidae	Rhinotermitidae	Termitidae
Comparison of traps (RD-I vs. RD-II)				
2 years pooled; individual numbers				
Correlation Coefficient	0.015	0.185	0.200	0.123
<i>P</i> value	0.840	0.014	0.008	0.105
Number of samples (n)	176	176	176	176
2 years pooled; presence/absence data set				
Correlation Coefficient		0.077	0.194	-0.029
<i>P</i> value		0.312	0.0.10	0.704
Number of samples (n)		176	176	176
2 years pooled; frequencies				
Correlation Coefficient		0.568	0.259	0.195
<i>P</i> value		<0.999	<0.005	<0.005
Number of samples (n)		25	25	25
1991–92; individual numbers				
Correlation Coefficient		0.198	0.204	0.193
<i>P</i> value		<0.005	<0.005	<0.005
Number of samples (n)		92	92	92
1992–93; individual numbers				
Correlation Coefficient		0.091	0.176	0.058
<i>P</i> value		<0.005	<0.005	<0.005
Number of samples (n)		81	81	81
Comparison of years: 1991–92 vs. 1992–93				
Trap RD-I; individual numbers				
Correlation Coefficient		0.311	0.246	0.189
<i>P</i> value		<0.005	<0.005	<0.005
Number of samples (n)		71	71	71
Trap RD-II; individual numbers				
Correlation Coefficient		0.060	0.141	0.114
<i>P</i> value		<0.005	<0.005	<0.005
Number of samples (n)		71	71	71