Swarming Behaviour and Alate Sex-Ratio of *Heterotermes indicola* (Wasmann) (Isoptera: Rhinotermitidae)

AYESHA AIHETASHAM* AND MUHAMMAD SAEED AKHTAR

Department of Zoology, University of the Punjab, Quaid-e-Azam Campus, Lahore 54590, Pakistan

Abstracts.- Swarming behaviour of *Heterotermes indicola* (Wasmann) was observed during the swarming season of 2003 and 2004 in the Punjab University, New Campus, Lahore, Pakistan. Swarming took place on 15 out of 92 nights for which observations were made. Swarming started after 3rd rainfall of the season, which created suitable combination of relative humidity and temperature required for swarming. Peak emergence of alates was observed after heavy rainfall (16mm) of short duration at 25.7°C to 36°C with 100% humidity. Frequency of swarming was maximum between 8:00 to 8:30 P.M. Overall sex ratio of *H. indicola* indicates that males dominate over females 5:1 (Male: Female).

Key words: Alates, Heterotermes indicola (Wasmann), sex-ratio, swarming behaviour.

INTRODUCTION

Swarming is an important event in the biology of termites during which males and females emerge from the nests, mate and establish colonies. The swarming period provides the only occasion when observations can be made undisturbed on many species of termites (Nutting, 1966). Few studies are available on swarming of termites in Pakistan (Akhtar, 1978; Afzal, 1983, 1984; Akhtar and Amanullah, 1989; Akhtar and Shahid, 1990; Ravan and Akhtar, 1999), compared to those done in other parts of the world (Nalepa *et al.*, 2001; Jones and Nalepa, 2002; Martius, 2001, 2003; Park *et al.*, 2004; only recent studies have been cited).

In Pakistan swarming of termites has been observed after rain often on hot and humid days. Termites do not swarm only on rainy day, but also six and seven days after the rain. When humidity of the atmosphere decreases appreciably, the swarming stops till the next rain (Akhtar, 1978).

In this study we report the impact of different environmental factors regulating the swarming pattern of *Heterotermes indicola* (Wasmann) in a specified plot in Lahore.

MATERIALS AND METHODS

A plot (100x100 meter) was selected in the new campus area near canal. For collection of

0030-9923/2008/0002-0075 \$ 8.00/0

Copyright 2008 Zoological Society of Pakistan.

swarming termites, a light trap of 200 watt was installed in specified plot and was posted 3.5 feet high from the ground. Each day from June 1st, 2003/ 2004 to August 31, 2003/2004, observations for the collection of swarming alates, irrespective of rainfall were made from sunset till 11:00 PM at night. Number of alates collected at light trap during every 30 minute were kept separate to know the peak emergence of alates of H. indicola. Besides, daily record of environmental factors *i.e.*, rainfall, atmospheric temperature, soil temperature, relative humidity etc. was also kept to see their effect on swarming. The data of environmental factors were obtained from the Regional Meterological Centre, Lahore. Imagoes collected both manually and with the container, from the light trap were preserved in 80% ethanol for further studies in the laboratory. Imagoes were sexed on the basis of width of seventh sternum, which is broader in females than in males. Females had dark brown thick outline on the abdomen. Data regarding production of alates in relation to environmental conditions were analyzed for correlation coefficient.

RESULTS

During 2003, flights of *H. indicola* were recorded around the specified plot on only fifteen of ninety two nights of observations. A total of 15 swarms of *H. indicola* were observed. Basic data

^{*} Corresponding author: e-mail misswaqar@yahoo.com

Date	Time of start of swarming PM	Soil temp. (°C)	Atmospheric temp. (°C)	Relative humidity %	Rainfall mm	Heterotermes indicola (wasmann)				
						Male		Female		
						No.	%	No.	%	Total
17-7-03	8:00	29.70	35.4	92	0.0	253	7.61	17	3.29	270
21-7-03	8:30	31.50	37.1	96	0.0	178	5.36	15	2.90	193
23-7-03	7:30	31.60	34	62	0.0	316	9.51	15	2.90	331
24-7-03	8:00	30.60	35	89	1.0	140	4.21	11	2.13	151
25-7-03	8:00	31.70	34.8	60	60.0	480	14.45	23	4.46	503
26-7-03	7:40	31.60	36.5	85	0.0	391	11.77	30	5.81	421
27-7-03	7:30	31.70	36	100	16.0	487	14.66	17	3.29	504
29-7-03	7:30	32.60	35.2	59	0.0	401	12.07	28	5.43	429
31-7-03	7:10	29.80	35.1	62	0.0	240	7.22	14	5.81	254
4-8-03	7:40	31.0	32.4	67	9.7	59	1.77	44	8.52	103
5-8-03	7:30	30.7	33.1	67	0.0	110	3.31	79	15.31	189
6-8-03	7:45	30.5	34	60	0.0	74	2.22	53	10.27	128
10-8-03	7:30	31.7	37	72	9.0	72	2.17	71	13.75	143
11-8-03	7:30	32.2	33.5	54	0.0	53	1.59	48	9.30	101
12-8-03	7:40	32.4	36.5	50	0.0	68	2.04	35	6.78	103
Total						3322		500		3822

regarding the number of alates collected on different dates and times along with environmental factors is

shown in Table I.

 Table I. Relationship of different environmental factors with number of alates in Lahore (Pakistan) during 2003 at canal bank, New campus, Lahore.

Correlation coefficient:

Soil temperature vs. total number of alates =0.187; Atmospheric temperature vs. total number of alates =0.264;

Relative humidity vs. total number of alates =0.143; Rainfall vs. total number of alates =0.505

During 2003, the first swarming took place on July 17 at 35.4°C atmospheric temperature and 92% relative humidity. Before the beginning of swarming, two sporadic rains of light intensity occurred in the studying area on July 14 and 15 and increased the atmospheric humidity. Maximum number of alates – 503 and 504 were collected respectively, on July 25 and 27 at 34.8 and 36°C atmospheric temperature and at 60 and 100% relative humidity (Table I, Fig. 1). A total of 3822 alates were collected during the swarming season of 2003. The swarming dates in relation to maximum and minimum atmospheric temperatures during 2003 and 2004 (data from Regional Metrological Centre) are shown in Figure 2.

The swarming behavior of *H. indicola* was also studied in 2004. The first swarming was observed on July 19, 2004 at 36° C atmospheric temperature and 47% relative humidity after two sporadic rains in the area on July 16 and July 17, 2004. The swarming period lasted from July 19,

2004 to August 2, 2004. During this period, 1677 alates were collected.

It rained more in 2003 than 2004. The data regarding the number of alates collected at different times and dates along with environmental factors are given in Table II and Figure 3.

During the study period of 2003, a total of 3822 alates of *H. indicola* were collected and atmospheric temperature ranged from 32.4° C to 37° C and soil temperature from 29.70° C to 32.60° C, while during 2004, atmospheric temperature ranged from 29.3° C to 38° C and soil temperature from 29.30° C to 33.70° C. Maximum swarming of the species occurred on July 27, 2003 at 100% relative humidity when there was 16 mm rainfall and atmospheric temperature 31.70° C. During 2004, maximum swarming of *H. indicola* was witnessed on July 19, 2004 at 47% relative humidity, 0.0 mm rainfall and 36° C atmospheric temperature.

Swarming of H. indicola in relation to

environmental factors

During the swarming period of 2003, atmospheric temperature ranged from 32.4°C to 37.1°C but the soil temperature ranged from

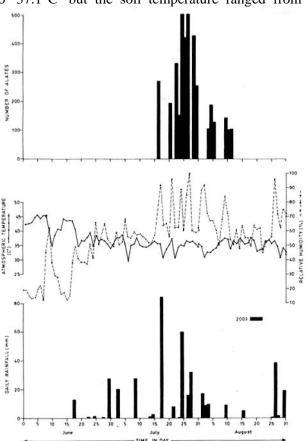


Fig 1. Number of alates of *H. indicola* (Wasmann) in relation to rainfall, atmospheric temperature and relative humidity during 2003.

29.70°C to 32.60°C. Coefficient of correlations between number of alates collected at different atmospheric temperatures (r = 0.264; d.f. = 13 P>0.05), between number of alates and soil temperature (r = 0.187; d.f. = 13 P>0.05), between number of alates and relative humidity (r = 0.143; d.f. = 13; P>0.05), and between number of alates and daily rainfall (r = 0.505; d.f. = 13; P>0.05) were positive but non significant.

Maximum emergence of alates was recorded during 3^{rd} and 4^{th} week of July 2003 and 1^{st} and 2^{nd} week of August, 2003. The minimum number of alates was collected on August 11, 2003 at 33.5° C atmospheric temperature and 54% relative humidity. Swarming almost ceased during the last two weeks of August. This decline in swarming could be because most of the swarming had already taken place or a critical combination of temperature and relative humidity did not develop which was necessary for swarming.

During 2004, swarming of *H. indicola* started on July 19, 2004 at 36°C and 47% relative humidity just after two rainfalls. Swarming continued for 5 consecutive days. Maximum number of alates was collected on July 19, 2004. The minimum number of alates was collected on July 30, 2004 at 34.3°C atmospheric temperature and 77% relative humidity.

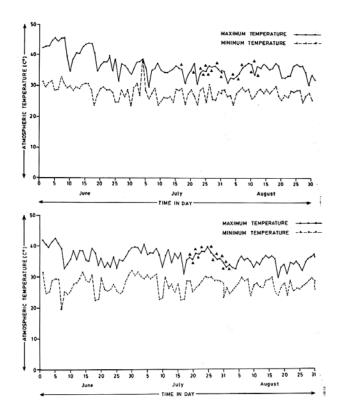


Fig. 2. Swarming dates of *H. indicola* (Wasmann) in relation to atmospheric temperature (Maximum and Minimum Temperature) data collected from Regional Meterological Centre, Lahore during 2003 (top) and 2004 (bottom).

Coefficient of correlations between number of alates collected at different atmospheric temperature was positive but non significant (r = 0.048; d.f. = 10, P>0.05), between number of alates and soil temperature (r = -0.346; d.f. = 10; P>0.05),

(r = -0.577; d.f. = 10; P < 0.05), between number of

and some imperature (1 = -0.540, 0.1. = 10, 1.2005),

between number of alates and relative humidity

 Table II. Relationship of different environmental factors with number of alates in Lahore (Pakistan) during 2004 at canal bank, New campus, Lahore.

Date	Time of start of swarming PM	Soil temp. (°C)	Atmospheric temp. (°C)	Relative humidity %	Rainfall – mm –	Heterotermes indicola (wasmann)				
						Male		Female		
						No.	%	No.	%	Total
19-7-04	7:45	31.00	36.0	47	0.0	202	15.44	8	2.17	210
20-7-04	7:40	30.80	35.3	55	0.0	157	12.00	5	1.35	162
21-7-04	7:40	31.50	37.2	32	0.2	191	14.60	11	2.98	202
22-7-04	8:00	31.00	37.1	40	0.0	129	9.86	7	1.90	136
23-7-04	7:45	31.80	38.0	42	0.0	121	9.25	3	0.81	124
26-7-04	7:30	33.00	37.8	58	0.0	134	10.24	2	0.54	136
27-7-04	7:40	33.70	36.6	62	0.0	90	6.88	7	1.90	97
28-7-04	7:30	33.00	35.2	63	0.0	98	7.49	3	0.81	101
30-7-04	7:45	30.00	34.3	77	0.0	28	2.14	66	17.87	94
31-7-04	7:30	29.3	29.3	67	55	43	3.29	117	31.70	160
1-8-04	7:40	32.7	32.7	100	0.0	50	3.82	58	15.71	108
2-8-04	7:30	33.6	33.6	64	22.8	65	4.97	82	22.22	147
Total						1308		369		1677

Correlation coefficient:

Soil temperature vs. total number of alates = -0.346; Atmospheric temperature vs. total number of alates = 0.048; Relative humidity vs. total number of alates = -0.577; Rainfall vs. total number of alates = 0.183

 Table III. Frequency of swarming and number of alates of *H. indicola* (Wasmann) at different times during study period of 2003-2004 (based on data of two years).

C. No	Time of amounting (DM)	S	No. of	alates	Total number of alates	
Sr. No.	Time of swarming (P.M.)	Swarming frequency —	2003	2004		
1.	6:30-7:00	_	_	_	_	
2.	7:00-7:30	1	62	-	62	
3.	7:30-8:00	2	575	405	980	
4.	8:00-8:30	6	1199	457	1656	
5.	8:30-9:00	5	1085	397	1369	
6.	9:00-9:30	3	901	418	1319	
7.	9:30-10:00	-	-	-	-	
8.	10:00-10:30	-	-	-	-	
9.	10:30-11:00	-	-	-	-	
	Total		3822	1677	5499	

alates and daily rainfall were non significant (r = 0.183; d.f. = 10; P<0.05). The data shows that higher relative humidity and high temperature favour swarming of *H. indicola*.

Frequency of swarms at different times during the swarming season of 2003-2004 is given in Table III. *H. indicola* swarms between 7:00-9:30 PM. Maximum frequency (6) of swarms were observed between 8:00-8:30 PM and a total of 1656 alates of *H. indicola* were collected during this time (Table III). Five swarms of *H. indicola* were observed from 8:30-9:00 PM and a total of 1369 alates were collected. Only 3 swarms of *H. indicola* were observed from 9:00-9:30 PM and a total of 1319 alates were collected. Relationship between flight times of *H. indicola* and sunset time in Lahore

(Pakistan) is shown in Figure 4. Majority of swarms of *H. indicola* were observed just after sunset and no swarming was observed before sunset. Swarming of *H. indicola* continued up to 9:30 PM and no swarming of this species was witnessed after 9:30 PM to 11:00 PM.

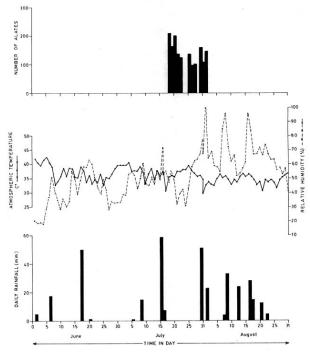


Fig. 3: Number of alates of *H. indicola* (Wasmann) in relation to rainfall, atmospheric temperature and relative humidity during 2004.

Sex ratio

Present studies with *H. indicola* revealed that sex ratio of the collected alate population was 5:1 (Male: Female) indicating dominance of males over females.

DISCUSSION

Dispersal is the primary purpose for swarming (Raina *et al.*, 2003). Swarming is probably controlled by endogenous biological clocks, along with the intrinsic mechanisms (colony regulating) and extrinsic factors (temperature, humidity and rainfall) (Ferraz and Cancello, 2001). Flight is essentially seasonal phenomenon. Medeiros *et al.* (1999) reported termite swarming in the Atlantic rain forest of Northeastern Brazil during November to July, with a high incidence at the beginning of the rainy season, March through May. Ferraz and Cancello (2001) investigated some aspects of swarming behaviour of *Coptotermes havilandi* in Brazil during 1997. They reported peak swarming of *C. havilandi* from August to October (end of winter and beginning of spring). It was also reported about sporadic smaller swarming almost all the year. A clear lapse in flight behaviour occurred only in May/June (autumn). Kumar and Sen-Serma (1987) reported swarming of *Odontotermes distans* from last week of February to last week of March in India.

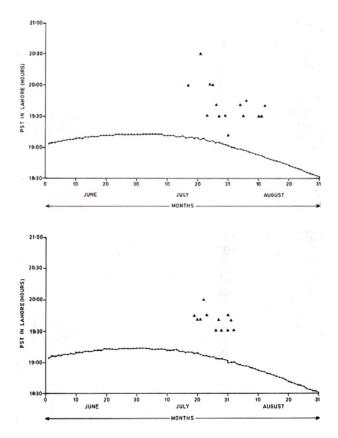


Fig. 4. Relationship between observed times of flight of *H. indicola* (Wasmann) and sunset times in Lahore (Pakistan) during study period of 2003 (top) and 2004 (bottom).

Weesner (1965) has noticed the flights of *Reticulitermes tabialis* from late winter to spring and again in fall. Noirot (1961) reported that in the tropics, where seasons are not sharply divided by temperature, the flights of many termites are

variously scheduled about a single rainy season. In regions with definite, cold winters and evenly distributed rainfall, alates production and flight of the entire fauna are restricted to the warmer summer months (Grasse, 1949; Noirot, 1961). Raina et al. (2003) reported that the swarming of alates of Coptotermes formosanus Shiraki, occurs around dusk during April to June in Louisiana and adjoining states. Martius (2001) reported that alate swarming occurs throughout the year and is probably related with rainfall. Ravan and Akhtar (1996) reported that the swarming of termites in Iran was witnessed from March to May, much earlier than that of Pakistan. Rebello and Martius (1994) analyzed the flight patterns of alates of termites in central Amazonia and reported frequency of swarming showed peaks at the beginning and the end of the rainy season (September/October to Decmber and April/May to June). However, in the middle of rainy season frequency was lowest. It was also recorded that frequency of swarming was low during the months when the forest was flooded (April to August). Martius (2003) reported that swarming was non linearly dependent on intermediate daily rainfall. In Pakistan, flights of termites are associated with summer rains. Ahmad et al. (1979) reported that whenever it rained moderately the swarming of Bifiditermes beesoni occurred on several consecutive days. Akhtar and Amanullah (1989) reported that swarming of *Coptotermes* heimi. Microtermes obesi. unicolor and Microcerotermes *Eremotermes* paradoxalis started after second rainfall of the season, which created a suitable combination of relative humidity and atmospheric temperature. Akhtar and Shahid (1990) have recorded 79 flights of seven species of termites. They reported that during 1985, the locality received abnormally high rainfall and swarming was initiated after fourth rain of the season.

Present studies on swarming behavior of *H. indicola* revealed that swarming was confined to summer months (July and August). It was recorded that swarming took place after two sporadic rains of light intensity with the gap of two days of the season of 2003 and after two consecutive rainfalls during 2004. The number of swarming individuals during 2003 was higher than that of 2004. This was most

probably because of more rains during 2003 as compare to 2004. The temperature and humidity conditions ranged from 32.4° C to 37.1° C and 50%to 100% during 2003, however, during 2004, temperature and humidity ranged from 29.3°C to 38°C and 32% to 100%. The temperature factor plays an important role in promoting reproductive isolation in different closely related species of termites. Many observers have recorded the range of temperature during flight of a particular species. Shi *et al.* (1987) recorded swarming of *O. hainanensis* from mid May to early June when daily mean temperature was 24.0°C to 26.8°C and relative humidity between 90.0 to 97.0%.

Akhtar and Shahid (1990) recorded swarming of different species between 25.5° C and 38° C atmospheric temperature, but the maximum swarming was observed from 25.5° C to 30.0° C. They have recorded that *O. lokanandi* swarms at atmospheric temperature of 25.5° C, which was lowest recorded temperature during the swarming season. Afzal (1981) stated that time of emergence of *B. beesoni* in field colonies was different from that of Laboratory colonies. He stated that in field colonies emergence always initiated after sunset, whereas in laboratory colonies emergence began several minutes before sunset.

Studies on Heterotermes indicola revealed that the swarming of alates of H. indicola starts at 7:10 PM just after sunset and continued up to 9:20 PM under suitable environmental condition. Raina et al. (2003) reported that swarming of alates of C. formosanus started around 8:00 PM and although most of the activity was over within one hour, some minor activity could be noticed almost until midnight. Ferraz and Cancello (2001) reported that the flight period preferred by C. havilandi in Brazil was around sunset. Alates show positive phototaxis and generally fly to the nearest source of light (Raina et al., 2003). The alates after flight around the nearest light source for several minutes land on the ground and lose their wings. Nutting (1969) suggested that the production of alates in most termites is controlled by pheromones and nutrients. Colony age, which is a measure of its size or maturity, appears to be fundamental determinant in alate production.

Roonwal (1960) recorded 18-43.3% of alates in colony of *O. obesus*. Gay and Greaves (1940) recorded over 6,600 alates from a mound of *C. lacteus* (Froggatt) that contained, one million termites. Sands (1965) estimated that 950 alates were produced from a mound of *T. ebenerianus* Sjostedt. Rebello and Martius (1994) recorded 2476 alates in Varzea and 8294 alates in Terra frime (Central Amazonia). Present studies carried out during 2003/2004, a total of 5499 alates of *H. indicola* were collected from a total of 27 swarming days.

As regards sex ratio, Henderson (1996) reported sex ratio of 50% males and 50% females of Formosan subterranean termite for most nights in New Orleans, USA. Ferraz and Cancello (2001) reported that sex ratio of alates of *C. havilandi* was close to 50:50 in Brazil. Mederios *et al.* (1999) reported over all sex ratio of the collected alate population of alates of twenty four morpho-species of the families Kalotermitidae, Rhinotermitidae and Termitidae was 1:1. Su and Scheffrahn (1987) reported overall sex ratio of the collected alate population of *C. formosanus* was 1:3 (F:M).

Henderson and Delaplane (1994) stated that sex ratio of light trapped alates varies over time but is generally female-biased, especially at the height of the flight season. Present studies with *H. indicola* also shows females dominated at the height of the flight season. Ravan and Akhtar (1999) reported that in case of *Postelectrotermes vagans* (Hagen), the sex ratio was 2:1 (M:F). For *Anacanthotermes vagans* (Hagen) the sex ratio was 2:1 (M:F) and for *Microcerotermes diversus* (Silvestri) it was 3:1 (M:F).

Present studies with *H. indicola* revealed that sex ratio of the collected alate population was 5:1 (M:F) indicating dominance of males.

REFERENCES

- AFZAL, M., 1981. *Studies on the biology of* Bifiditermes beesoni (Gardner). Ph.D. thesis, University of the Punjab, Lahore, Pakistan.
- AFZAL, M., 1983. Inability of swarming alates of dry wood termite *Bifiditermes beesoni* (Gardner) (Isoptera), II. Mutual feeding potentialities of soldier and nymphs.*Material und Organismen*, **18**: 107-117.
- AFZAL, M., 1984. Studies on colony founding behaviors of

Bifiditermes beesoni (Gardner) (Isoptera: Kalotermitidae). Z. angew. Ent. (J. appl. Ent.), **98**: 310-316.

- AHMAD, M., SHEIKH, K.H. AND JAFRI, R.H., 1979. Biology, pathology and distribution (in relation to soil conditions) of termites of Pakistan. Project No. 17-FS-21, pp. 1-424.
- AKHTAR, M.S., 1978. Some observations on swarming and development of incipient colonies of termites of Pakistan. *Pakistan J. Zool.*, **10**: 283-290.
- AKHTAR, M.S. AND AMANULLAH, 1989. Swarming behavior of termites of Punjab University, New Campus, Lahore. *Pakistan J. Zool.*, 21: 229-237.
- AKHTAR, M.S. AND SHAHID, M.M., 1990. Impact of rainfall, atmospheric and wind speed on swarming of termites (Isoptera). *Pakistan J. Zool.*, **22:** 65-80.
- FEI, H.X. AND HENDERSON, G., 1999. Effect of moisture and two nitrogen sources on nest site choice by alates and dealates of *Coptotermes formosanus* in the laboratory (Isoptera: Rhinotermitidae). *Sociobiology*, 34: 581-589.
- FERRAZ, M.V. AND CANCELLO, E.M., 2001. Swarming behavior of the economically most important termite, *Coptotermes havilandi* (Isoptera: Rhinotermitidae), in south Eastern Brazil. Sociobiology, 38(3B): 683-694.
- GAY, F.J. AND GREAVES, T., 1940. The population of a mound colony of *Coptotermes lacteus* (Frogg.). J. *Coun. scient. indust.. Res. Aust.*, **13**: 145-149.
- GRASSE, P.P., 1949. Ordre des Isoptera ou termites. In: Traite de Zoologie (ed. P.P. Grasse), vol. 9, pp. 408-544. Masson, Paris.
- HARRIS, W.A., 1961. *Termites: their recognition and control*. Longmans, Green and Co., London.
- HARRIS, M.V. AND SANDS, W.A., 1965. The social organization of termite colonies. *Symp. zool. Soc. London*, **14**: 113-131.
- HENDERSON, G., 1996. Alate production, flight phenology and sex-ratio in *Coptotermes formosanus* Shiraki, an introduced subterranean termite in New Orleans, Louisiana. *Sociobiology*, 28: 319-326.
- HENDERSON G. AND DELAPLANE, K.S., 1994. Formosan subterranean termite swarming behavior and alate sexratio (Isoptera: Rhinotermitidae). *Insectes Sociaux*, 41: 19-28.
- JOHNSON, G.C., 1966. A functional system adaptive dispersal by flight. *Annu. Rev. Ent.*, **31:** 233-260.
- JONES, S.C. AND NALEPA, C.A., 2002. Survey of the termite (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of St. John, US Virgin Islands. Sociobiology, 39: 155-163.
- KUMAR, S. AND SEN-SERMA, P.K., 1987. Some observations on swarming behavior, sex ratio, sexual dimorphism and moisture content in *Odontotermes distans* Holmgren and Holmgren (Isoptera: Macrotermitinae). Ann. Ent., 5: 57-60.
- KUMAR, S. AND THAKUR, M.L., 1990. Observations on

swarming characteristics of *Microcerotermes beesoni* Snyder in nature (Isoptera: Termitidae: Amitermitinae) in Doon Valley. *Indian J. Fores.*, **13**: 210-213.

- LEONG, K.L.H., TAMASHIRO, J.Y. AND SU, N.Y., 1983. Micro-environmental factors regulating the flight of *Coptotermes formosanus* Shiraki in Hawaii (Isoptera: Rhinotermitidae). *Proc. Hawaii ent. Soc.*, 24: 287-292.
- MARTIUS, C., 2001. Observation of alate swarming and colony foundation in *Syntermes spinosus* (Isoptera: Termitidae) in Amazonia. *Sociobiology*, **37**(3B): 585-591.
- MARTIUS, C., 2003. Rainfall and air humidity: non-linear relationships with termite swarming in Amazonia. *Amazon. Limnol. Ecol. Reg. Syst. Flum. Amazonas*, 17: 387-397.
- MEDEIROS, L.C.D., BANDEIRA, A.G. AND MARTIUS, C., 1999. Termite swarming in the northeastern Atlantic rain forest of Brazil. *Stud. Neotrop. Fauna Environ.*, 34: 76-87.
- MILL, A.E., 1983. Observations on Brazilian termite alate swarms and some structures used in the Dispersal of reproductives (Isoptera: Termitidae). J. Nat. Hist., 17: 309.
- NALEPA, C.A., MILLER, L.R. AND LENZ, M., 2001. Flight characteristics of *Mastotermes darwiniensis* (Isoptera: Mastotermitidae). *Insectes Sociaux*, **48**: 144-148.
- NOIROT, C., 1961. Le cycle saisonnier chezles termites. Proc. 11th Intr. Cong. Entomol., Vienna, 1960, **1:** 583-585.
- NUTTING, W.L., 1966. Colonizing flights and associated activities of termites 1. The desert damp wood termite, *Paraneotermes simplicicornis* (Kalotermitidae). *Psyche*, **73:** 131-149.
- NUTTING, W.L., 1969. Flight and colony foundation. In: *Biology of termites* (eds. K. Krishna and F.M. Weesner). Academic Press, New York and London vol. 1, pp. 233-282.
- PARK, Y.I., BLAND, J.M. AND RAINA, A.K., 2004. Factors affecting post flight behavior in primary reproductive of the Formosan subterranean termite, *Coptotermes formosanus* (Isoptera: Rhinotermitidae). J. Insect Physiol., **50**: 539-546.
- RAINA, A., PARK, Y.I. AND FLORANE, C., 2003. Behavior and reproductive biology of the primary reproductive of the Formosan subterranean termites (Isoptera: Rhinotermitidae). *Sociobiology*, **41**: 37-48.

- RAINA, A.K., BLAND, J.M., DICKEN, J.C., PARK, Y.I. AND HOLLISTER, B., 2003. Premating behavior of Dealates of the Formosan subterranean termite and evidence for the presence of a contact sex pheromone. *J. Insect. Behav.*, 16: 233-245.
- RAVAN, S. AND AKHTAR, M.S., 1996. Swarming behavior of termites (Isoptera) in the Province of Sistan and Baluchistan (Zabul), Iran. *Pakistan J. Zool.*, 28: 85-95.
- RAVAN, S. AND AKHTAR, M.S., 1999. Swarming of nymphs of *Postelectrotermes pasniensis* (Isoptera: Kalotermitidae). *Sociobiology*, **33**: 105-109.
- REBELLO, A.M.C. AND MARTIUS, C., 1994. Dispersal flights of termites in Amazonian forests (Isoptera). *Sociobiology*, 24: 127-146.
- ROONWAL, M.L., 1960. Biology and ecology of oriental termites No. 5. Mound structure, nest and moisturecontent of fungus combs in *Odontotermes obesus*, with a discussion on the association of fungi with termites. *Rec. Ind. Mus.*, 58: 131-150.
- SANDS, W.A., 1965. Alates development and colony foundation in five species of *Trinervitermes* (Isoptera: Nasutitermitinae) in Nigeria, West Africa. *Insects Sociaux*, **12**: 117-130.
- SHI, J.X., LI, D., ZHANG, J.F. AND CHEN, Y.H., 1987. Observations on the emergence and swarming of Odontotermes hainanensis Light. Insect Know., 24: 337-343.
- SU, N.Y. AND SCHEFFRAHN, R.H., 1987. Alate production of a field colony of the Formosan subterranean termite (Isoptera: Rhinotermitidae). *Sociobiology*, **13**(2): 167-172.
- SU, N.Y., SCHEFFRAHN, R.H. AND BAN, P.M., 1989. Methods to monitor initiation of aerial infestations by alates of the Formosan subterranean termite (Isoptera: Rhinotermitidae) in high-rise buildings. J. econ. Ent., 82: 1643-1645.
- THORNE, B.L., 1983. Alate production and sex ratio in colonies of the Neotropical termite *Nasutitermes corniger* (Isoptera: Termitidae). *Oecologia*, **58**: 103.
- WEESNER, F.M., 1965. The termites of the United States. A handbook of National Pest Control Association. Elizabeth, New Jersey.

(Received 23 April 2007; revised 11 December 2007)