

# REPRODUCTIVE SYNCHRONIZATION IN THE TROPICS: THE CIRCA-SEMIANNUAL RHYTHM IN THE NUPTIAL FLIGHT OF THE GIANT ANT *CAMPONOTUS GIGAS* LATREILLE (HYMENOPTERA, FORMICIDAE)

Martin Pfeiffer & K. Eduard Linsenmair

Theodor-Boveri-Institut für Biowissenschaften der Universität Würzburg, Lehrstuhl für Tierökologie und Tropenbiologie, Am Hubland, 97074 Würzburg, Germany

**Abstract.** The nuptial flight of the polydomous giant ant *Camponotus gigas* Latreille 1802 in the lowland dipterocarp forest of Kinabalu National Park, Sabah, Malaysia and its periodicity are described. In total we recorded 29 flights. In three flights the observed number of winged sexual forms swarming from one colony ranged between 10 and 200 reproductives. The mating flights started at 16:30 h, i.e., around 1¼ hours prior to the beginning of the nocturnal activity period of the foragers, and ended around 20:00 hours. Over five years we noted 26 additional flights mostly at artificial light sources. The flights took place during the whole year except for April (with no observations made in August). Four of the directly observed flights were 188 days apart from each other, a fifth 382 days. The temporal occurrence of 12 nuptial flights was statistically analyzed by probability calculus. A period of  $188 \pm 5$  days for each cycle proved to be highly significant. Altogether 15 flights could be fitted to five overlapping cycles. Other data from Sabah, which also support the assumption of a circa-semiannual reproductive cycle, are discussed. Accepted 7 May 1997.

**Key words:** *Camponotus*, *Formicidae*, mating flights, phenology, periodicity, aseasonality, circa-semiannual rhythm, phase shifted reproductive cycles, tropical rain forest, Borneo.

## INTRODUCTION

In temperate latitudes individuals of outbreeding populations have to synchronize their activity not only with that of the opposite sex but also with the geophysical course of the year, with its marked seasonal changes and dramatically changing environmental conditions. The most important *zeitgeber* for temperate species is the annual photoperiodic cycle (Gwinner 1986, Palmer 1976) often modified by temperature cycles (Müller 1992). In the equatorial tropics, however, the daily photoperiodic alteration within the year is limited, thus giving hardly any guide to the season, which could serve as a proximate releaser for physiological activity. Since most other environmental clues, like temperature or rainfall, are either constant or unpredictable, exact *zeitgebers* seem to be lacking near the equator. However, the more aseasonal the environmental conditions become, the lower is the need for close synchronization with them. Species that gain independence from seasons may develop shorter reproductive cycles, and thus benefit in the reproductive competition with their interspecific seasonal rivals. However, detached from

synchrony with seasonality these organisms have to synchronize for reproduction.

Despite the limited seasonal variation – especially in the perhumid tropics – there exists a variety of mechanisms to achieve synchrony of reproductive activity within populations of different exogamous organisms (see e.g., Whitmore 1988 for a review of mechanisms in South-East Asian tropical plants).

Most tropical tree species show an annual pattern of phenology even in almost aseasonal climates. This seems to be triggered by a seasonality in radiation (van Schaik *et al.* 1993, Wright & van Schaik 1994) and shows strong phylogenetic patterns (Wright & Calderon 1995). In a Malaysian rain forest, the tree community as a whole exhibited regular seasonality, with a single annual peak of flowering and fruiting (Medway 1972). Other data from South-East Asia suggest two distinct peaks of tree flowering that coincide with the driest months of the year (Whitmore 1990).

Besides this annual periodicity many species exhibit supra-annual rhythms, e.g., several species of the dipterocarps that fruit heavily at irregular intervals of two to 10 years (Ashton *et al.* 1988). In some

of these plants endogenous rhythms seem to trigger flowering (e.g., bamboos with their extremely long periodicity; see Janzen 1976), in other cases flowering is determined by exogenous factors. In the Dipterocarpaceae, dry weather in "El Niño Years" precedes mass flowering (Whitmore 1990) that may be induced by a short drop in minimum night temperature for three or more nights (Ashton *et al.* 1988). Chilling of flower buds is a flowering stimulus in many orchids and trees (Murawski 1995).

In the presence of rather constant or unpredictable conditions, timing in animals is often achieved with endogenous "clocks". In tropical or migratory bird species, breeding and moulting are timed by endogenous circannual rhythms, which keep them synchronized with the course of the year (for review see Gwinner 1996). The same may be true for reproductive cycles of tropical mammals (O'Brian 1993). However, not all tropical rain forest animals show seasonal peaks in breeding. No trends to seasonality were shown in six species of frogs in Sarawak (Inger & Bacon 1968) or 10 species of lizards (Inger & Greenberg 1967). Aseasonal reproductive behavior was also found in the Malayan Barn Owl *Tyto alba* (Wells 1976) which is a year-round breeder, and in the African Bat Hawk *Machaerampus alcinus* that breeds in intervals shorter than one year (Hartley & Husler 1993). Nothing is known on how reproductive synchronization is achieved by these species.

Organisms with very brief periods of reproductive pairing should face special problems with synchronization. Many social insects reproduce during short mating flights, which take place only once or a few times within a year.

Most ant species are exogamous and invest very high amounts of energy and biomass into their winged sexuals (Hölldobler & Wilson 1990). In order to avoid the entire loss of this costly investment the precise timing of nuptial flights is of paramount importance. Of special significance for determining the right moment for the nuptial flight of a colony's winged reproductives is the very tight synchronization with the nuptial flights of at least some of the neighboring conspecific colonies, for the following reasons:

(1) Both sexes suffer high losses due to predation. High synchronization could serve as an anti-predator strategy by swamping the predators population. This kind of reproductive strategy is known in many species of ants and termites (Wilson 1975) and from

bamboo (Janzen 1976), as well as from the mass flowering of tropical trees (van Schaik *et al.* 1993, see also Kelly 1994).

(2) In most species of ants the males live only a few days, due to low investment in single individuals during development.

(3) To achieve exogamous pairing, male and female reproductives of different colonies have to be synchronously active to meet at the mating places.

In temperate latitudes ant reproduction is coupled with the annual cycle of colony development. Only a small part of all eggs, laid in limited periods of the year, will become sexuals (Hölldobler & Wilson 1990). The oviposition period of the mother queen seems to be either endogenously controlled by a circannual cycle that is triggered by temperature and photoperiod, or is entirely regulated by external ecological factors, above all by temperature (Kipyatkov 1993). In both cases development of sexuals is closely connected with the seasonality of the year. The triggering of swarming, which occurs within a fixed time-window is effected by changes of temperature and light intensity (Boomsma & Leusink 1981). For species that occupy dry habitats such as deserts and grasslands rain is one of the commonest triggers (Hölldobler & Wilson 1990). In the extremely diverse ant communities of evergreen tropical lowland rain forests (e.g., Floren & Linsenmair 1994, Wilson 1987; reviewed by Tobin 1995) very little is known about nuptial flights (Hölldobler & Wilson 1990) or annual cycles (review in Kipyatkov 1993).

*Camponotus gigas* Latreille 1802 occurs in tropical lowland forests of South-East Asia and is one of the largest ant species in the world. Its polydomous colonies comprise about 8000 foragers and cover territories up to about one hectare (Pfeiffer & Linsenmair unpubl. data). These mainly nocturnal ants forage in the forest canopy. Foragers leave their underground nests at dusk to invade the canopy in close columns (Chung & Mohamed 1993, Gault 1987, Orr & Charles 1994). Their diet consists mostly of honeydew obtained from tree-sucking Homoptera (Pfeiffer 1997).

During a long-term study on the behavioral ecology of *Camponotus gigas*, we recognized a recurrent periodicity of mating flights at one nest surveyed over five years. However, it seemed that there was no synchronization at the population level: we frequently sampled reproductives at light sources, yet without recording nuptial flights at the nests under direct observation. To examine whether the apparent pat-

tern was real, and whether there may be different cycles of reproduction within the population, we concentrated our study on determining the exact dates of departures at the nests and surveyed as many nuptial flights of *C. gigas* within the population as possible by means of light trapping.

## METHODS

*Observations.* The data presented here are part of a long-term study of *C. gigas* that was conducted from July 1991 to November 1995 in the lowland dipterocarp forest of Poring Hot Spring, Kinabalu National Park, Sabah, Malaysia at 6°5' N. Field observations were made during five extended visits from 28 July 1991 to 29 November 1991, 11 February 1992 to 7 May 1992, 9 September 1992 to 19 May 1993, 7 January 1994 to 12 July 1994, and 19 September 1995 to 12 November 1995.

We concentrated our study on 4 areas: a) the main nest of one *Camponotus gigas* colony (nest K), b) the 5 ha area of primary forest around nest K, c) the electrically illuminated "Hot Spring Area" (HSA) at the edge of the forest (500 m away from nest K), and d) a light source near our flat, also situated near the forest, but approximately 800 m away from the HSA. These sites were controlled nearly every day. Further data were collected at the main nest of another *C. gigas* colony. During our absence other members of our research team in Poring continued data collection and registered all nuptial flights. Furthermore, the capture dates of all mounted reproductives from the Forest Research Institute Sandakan and the Kinabalu Museum were recorded.

*Statistical analysis.* At first all flights were sorted as explained in the "results" section. Using this method of analyzing our data we were able to construct different cycles of mating activity with nearly identical period lengths. We then tested these periods for consistency with our hypothesis of regular flight intervals in individual colonies, but with only partial synchronization between different colonies within an area.

Although the nuptial flights of *C. gigas* at Poring seemed to be spread over five cycles, we tested the more conservative hypothesis that all observed flights would fit equally well in only two cycles by computing the flights of the other cycles against the tested pattern.

In this manner we tested only cycle I (mating flights of Nest K, mostly direct observations) and

cycle II (observations at artificial lights). The period of 188 days was initially deduced from the first two nuptial flights of cycle I. This period was omitted from the further analysis since it had served to formulate the hypothesis of a periodic circa-semiannual flight.

The time from 5 May 1992 until 11 November 1995 was divided into intervals of 11 days. Thereby 5 May 1992 was situated in the middle of interval  $I_{(0)}$ . Considering slight irregularities in the timing of the nuptial flights, which are common in such cases, we made an allowance of  $\pm 5$  days, which led to an 11 day interval. The interval length was more or less arbitrary; however, we considered the possibility that single deviations may add up over the years. This arrangement also included the periods with no observations. Out of all these periods we marked those which contained a day with an interval of 188 days (or a full multiple of it) either from 17 February 1992 (1st day of cycle II) or 5 May 1992 (1st day of cycle I).

Flight dates of cycles III, IV and V lay in one of the unmarked intervals, thus distributed against the tested pattern. All flights within one interval were counted as one flight. So we excluded all synchronous flights. After marking, we omitted all intervals which fell partly or fully in those time spans where no observations were made. Interval  $I_{(0)}$  was also discounted. By this procedure 45 intervals remained, seven of which were marked. Five out of 12 detected mating flights happened in marked intervals, seven in unmarked. If the null hypothesis of even distribution were true, then the 12 intervals had to be a mere random selection of all 45 intervals. The probability that there are at least five marked among the 12 intervals with mating flights can be calculated according to the hypergeometrical distribution (see Sokal & Rohlf 1995):

$$\frac{\binom{7}{5} \binom{38}{7}}{\binom{45}{12}} + \frac{\binom{7}{6} \binom{38}{6}}{\binom{45}{12}} + \frac{\binom{7}{7} \binom{38}{5}}{\binom{45}{12}} = 0.0099$$

This means that the null hypothesis of even distribution can be rejected with 99% probability.

Using this method we calculated the probability of two other flight cycles, which were constructed by evaluating data from museum specimens.

## RESULTS

*Behavior.* On three occasions we observed the nuptial flight directly at the nest. Between 100 and 300 workers left their nest around 16:30 h, approximately 1¼ hours prior to the normal evening start of foraging activity. They surrounded the nest area at the base of the nest tree and also climbed on the trunk of the tree. Fifteen minutes later the first winged sexuals appeared and gathered on the buttress roots of the nest tree. At the first flight 40 males appeared, at the second approximately 200 males and 25 queens. On the third occasion we counted approximately 100 males. Because of the steady movement of the ants exact counts were impossible. When it was getting dark, at around 17:30 h, the first males began swarming off. At the same time the queens and some of the males climbed up the tree to start from a greater height (above 6 m). Bats intensively hunted the rising swarm. At 19:00 h the majority of the winged ants had left and about 2/3 of the workers had returned to the nest. Remaining males were bitten several times by workers in their tarsi until they flew off. Compared to other days the nocturnal exodus of the foragers into the canopy was retarded by half an hour.

Males and females caught before departure at different nests remained sexually inactive when experimentally brought together in flight cages. Twenty-five males that we had caught at the nests and kept in cages survived a mean of 3.9 days (SD = 1.72), with a range of 1 to 8 days.

One mated queen climbed down near the nest directly after a mating flight, possibly indicating that queens may not fly very far. On several other occasions mated queens that had started at other colonies climbed down near the nests that were under our observation, but they avoided the nest entrances. One of these queens walked nearly 20 m on the busy trunk trail of the observed colony without being attacked. On two other occasions we collected altogether six mated queens, all climbing down different trees in our study area.

*Rhythms.* The directly observed nuptial flights showed a distinct periodicity. The first four flights – directly observed at the same individual colony – followed each other at intervals of exactly 188 days in length. On the last target date, on 16 May 1993 at 16:40 h, around 260 workers had spread over the tree trunk and the first males had just appeared at the nest entrance when a heavy downpour started.

Although the nest entrance was sheltered by an umbrella, the nuptial flight stopped and the ants swarmed back into their nest. Because of the heavy rain we had to stop our observation on that day. On the two following days we could not detect any flight activity at the nest, but we did notice males of *C. gigas* at the lights. Since we left Sabah on the third day, it remained unclear for how long the nuptial flight at nest K had been delayed. The next flight we observed at this nest did not take place as expected on 27 May, but 6 days later on 2 June 1994.

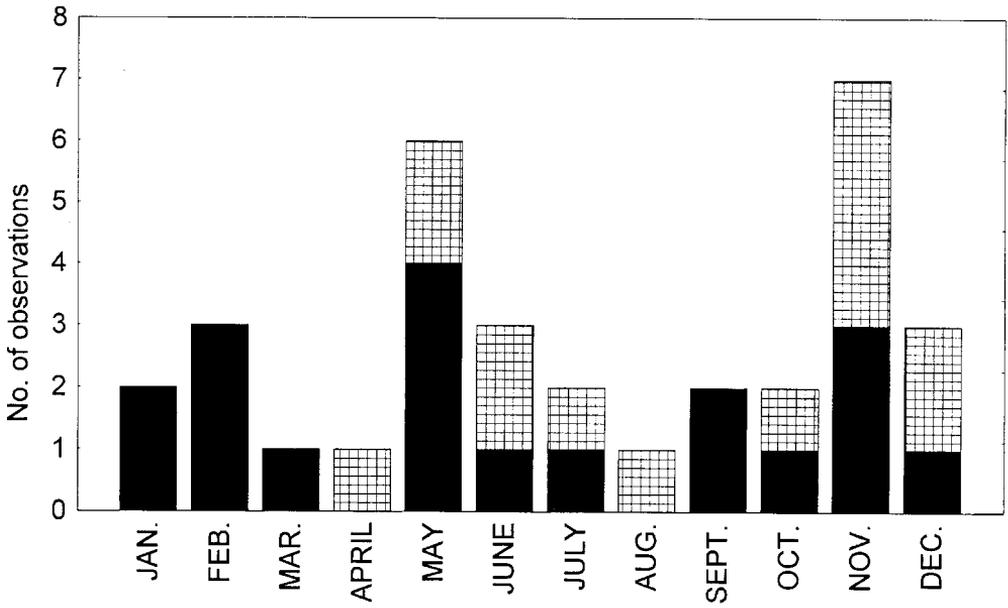
During the 1994 observation period, sexuals of *C. gigas* appeared at light sources in January, February, March, May and June, but we were unable to determine from how many nests these had come. On several occasions, when we had directly observed a mating flight at nest K, we also noticed winged reproductives (mostly males) at lights. Especially at the HSA there were generally swarms of about 30 males. However, swarms at the HSA did not necessarily indicate swarming at nest K. Eleven out of 29 observations (see Table 1) occurred synchronously with other records. With an allowance of  $\pm 1$  day, five further observations can be called synchronous. On 9 November 1992 we observed two synchronous mating flights at different colonies besides nests K and G. What are the mechanisms synchronizing nuptial flights? What might be the triggering factors?

Table 1 shows a list of our observations. Fig. 1a shows the yearly distribution of the recorded mating flights on a monthly scale. If, in addition, we take into consideration the sampling dates of the mounted species from the Forest Research Institute Sandakan and the Kinabalu Museum, the records show two peaks in May and November at the beginning of the two rainy seasons. We tested this assumption against the null hypothesis of even distribution of the flights within the year. The peaks proved not to be significant in a chi-square test (four periods of three months: 2–4, 5–7, 8–10, 11–1;  $df = 3$ ;  $\chi^2 = 5.18$ ;  $P = n.s.$ ). The nuptial flights seemed to occur, with similar probability, all the year round. From our observations we knew that heavy rain could prevent the reproductives from starting. Light rainfall did not appear to influence flight (see Table 1). Fig. 2 shows the precipitation during the 11 days before the flight, with a black square indicating the maximum within the last 2 days before the departure. In all cases this maximum was above the median of the full period showing that swarming usually took place after a short period of relatively heavy rain.

TABLE 1. Mating flights (MF) of *Camponotus gigas* in Poring Hot Spring from August 1991 to February 1996 showing the date on which the flights occurred, the number of the day of the year, whether flights were synchronized with other colonies (SYN), cycle number (Nr.; see Figure 3), the interval to the last flight of the same cycle, the lunar phase (day 1 is the first day after new moon), the precipitation on the day of flight and the preceding day, the location at which observations were made, and additional observations. Asterisks (\*) denote an observation of synchronized flight on the same day whereas a plus-minus sign ( $\pm$ ) denotes occurrence of synchronized flights on the day before or after. Discussion in the text. Locations were: observation area (OA), nest K, nest G, a light source near our flat (Flat) and the hot spring area (HSA).

#	Date	Day of the year	SYN	Nr.	Period of cycle interval [days]	Lunar-phase	Rain [mm]	Rain day before [mm]	Location	Observations
1	9 September 1991	252				1	Yes	Yes	OA	A wingless ♀ coming down the trunk of a tree.
2	30 October 1991	303		I	—	2n4	Yes	?	Nest K	40 ♂♂ start before 18:00 h.
3	17 February 1992	48		II	—	14	0.0	Yes	Flat	1 ♂ in our kitchen.
4	5 May 1992	126		I	188	3	0.0	Yes	Nest K	25 ♀♀ + 200 ♂♂, start before 19:00 h.
5	9 November 1992	314	*	I	188	15	0.6	17	Nest K	100 ♂♂ start before 19:00 h. Another nuptial flight at Nest G about 1 km away.
6	9 November 1992	314	*	I	188	15	0.6	17	Nest G	At 19:30 h approx. 50 ♂♂ + one ♀. At the same time mating flight at nest K.
7	14 November 1992	319	*	(I)	193	20	0.0	11.1	HSA	♂♂ at the lights (obs. by H. Wittekindt).
8	14 November 1992	319	*	(I)	193	20	0.0	11.1	Flat	♂♂ at the light (obs. by H. Wittekindt).
9	22 December 1992	356		III	—	16			OA	We caught a wingless ♀.
10	15 January 1993	15		IV	—	22	0	3.0	Flat	Several ♂♂ at the light.
11	16 May 1993	136	±	I	188	24	35	5.1	Nest K	Heavy rain stops the mating flight at 17:00 h. No departure.
12	17 May 1993	137	±	I	189 (184)	25	0.5	35.0	HSA	♂♂ at the lights.
13	18 May 1993	138	±	(I)	190 (185)	26	27.1	0.5	Flat	♂♂ at the light.
14	28 January 1994	28	*	IV	378 = 2 x 189	16	15.2	86.2	HSA	40 ♂♂ at the lights.
15	28 January 1994	28	*	IV	378 = 2 x 189	16	15.2	86.2	Flat	5 ♂♂ at the light.
16	6 February 1994	37				25	7.1	21.5	HSA	c. 300 ♂♂ in the open air kitchen of the hostel.
17	7 March 1994	66	*	II	749 = 4 x 187.25	25	0.0	18.4	OA	Two wingless ♀♀, coming from the canopy. At the same time MF at HSA and at our Flat.
18	7 March 1994	66	*	II	749	25	0.0	18.4	HSA	More than 50 ♂♂ at the lights.
19	7 March 1994	66	*	II	749	25	0.0	18.4	Flat	Many ♂♂ at the light.
20	1 May 1994	121		V	—	20	3.0	4.8	Flat	♂♂ at the light.
21	25 May 1994	145		I	374 = 2 x 187	15	0.0	1.8	OA	We caught a wingless ♀.
22	1 June 1994	152	±	I	380 =	22	29.7	21.2	HSA	♂♂ at the lights.
23	2 June 1994	153	±	I	382 = 2 x 191	23	0.5	29.7	Nest K	2 ♂♂, mating flight was discovered at 18:45 h only. Later we found 2 wingless ♀♀, crawling down the trunks of the highest trees.
24	25 July 1994	206		III	945 = 5 x 189	27			HSA	A dead ♀ was found by the pools (obs. by C. Brühl).
25	20 September 1994	263	*	II	562 = 3 x 187.3	26			HSA	c. 20 ♂♂ at the lights.
26	20 September 1994	263	*	II	562 = 3 x 187.3	26			Flat	♂♂ at the light.
27	24 September 1994	267		II	566 = 3 x 188.6	1			Flat	One ♂ at the light.
28	11 November 1995	315		V	559 = 3 x 186.3	18	0.0	Yes	Flat	A winged ♀ behind the house.
29	14 February 1996	45		IV	747 = 3 x 186.75	10	0.0	Yes, and the week before	Flat	♂♂ at the light (obs. A. Floren).

a)



b)

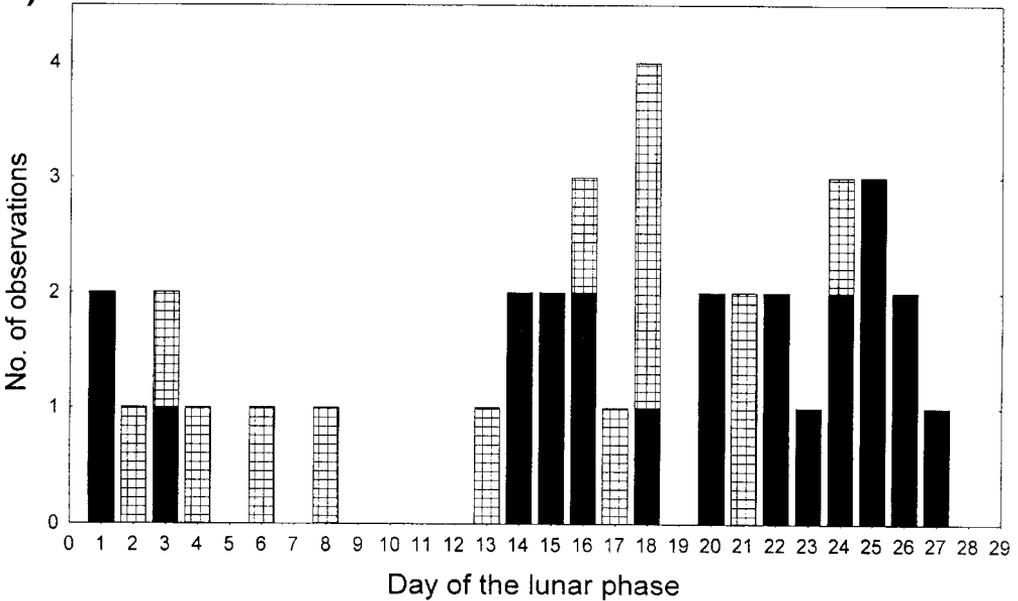


FIG. 1. a) Timing of *Camponotus gigas* nuptial flights on a monthly scale, over the course of the year (synchronous flights within five days counted once;  $df = 3$ ;  $\chi^2$  n.s.) and b) over the lunar cycle. Day 0 is new moon. The period of 11-25 days differs significantly from the rest of the cycle (synchronous flights within one day counted once;  $df = 1$ ;  $\chi^2$  6.08,  $P < 0.05$ ). Black bars: Timing of mating flights from Poring. Chequered bars: Timing of mounted reproductives from the Kinabalu Museum and the collection of the Forest Research Centre, Sandakan.

As *Camponotus gigas* is predominantly active at night, and the nuptial flights start at dusk, we examined possible influences of the lunar phase, which functions as a *zeitgeber* for synchronized rhythmic patterns of reproductive behavior in many other organisms (Neumann 1981). We tested the assumption that mating flights occurred significantly more often at full moon or as the moon wanes (day 11–25; see Fig. 1b) than during the rest of its cycle, against the null hypothesis of even distribution ( $df = 1$ ;  $\chi^2 = 6.08$ ;  $P < 0.05$ ).

At nest K we directly observed a rhythm of approximately 188 days. If this periodicity is taken as a base, several of the swarming dates that were monitored at the lights, or suggested by wingless queens we caught while they were descending from trees, can be related to each other. We tried to arrange them in periods of 188 days. Using five starting dates we arrived at five "cycles" of mating flights (see Fig. 3 and Table 1).

Starting from our direct observations at nests K and G, we related 12 observations to one semiannual cycle of nuptial flights with a period length of  $188 \pm 5$  days. On the assumption of four other cycles, with the same period length, we could insert 27 of our total of 29 records into a complex pattern.

We captured a mated queen on 25 May 1994. This was 374 days after the last directly observed mating flight at nest K on 16 May 1993 (cycle I, Tab. 1 line 21). This fits a cycle with a period length of  $2 \times 187$  days and may point to a nest initially synchronized with nest K. Three synchronous observations on 7 March 1994 (cycle II, Tab. 1 line 17–19) took place 910 days ( $= 4 \times 187.25$ ) after we found a male in our kitchen on 17 February 1992. The next observation of this cycle was on 20 September 1995, when we watched many males around the lights of our veranda. This event was 562 days after the 7 March 1994 observation, thus matching three periods of 187.3 days. Cycle III comprises two observations on 22 December 1992 and 25 July 1995. This interval of 945 days can be divided into five periods of 189 days. Cycle IV started with an observation on 15 January 1993, included two synchronous observations on 28 January 1994 (line 14, 15; interval length  $2 \times 189$  d) and ended with a complementary one on 14 February 1996 (interval length  $4 \times 186.75$  d). Cycle V had an interval length of  $3 \times 186.3$  days and was registered only at our veranda. (After we had finished our study our colleague Jan Beck recorded another flight of this cycle there on

20 November 1996; its interval length was  $2 \times 187.5$  d.)

After consideration of all synchronous flights, 17 independent flight dates were left. Only two of them could not be fitted into one of the suggested five cycles (see Fig. 3, Table 1). The phase-shifted cycles lay 43, 55, 68 and 110 days apart in relation to cycle I, so the mean difference between the flights was 35.8 days (S.D. = 24.6). Period length within the cycles varied between 187 and 191 days (mean = 188.12, S.D. = 1.520 for  $n = 26$  non-synchronous intervals). Using probability calculus we analyzed the distribution of 12 nuptial flights between just two cycles (see Methods). Even under these conservative conditions (in this calculation the flights of cycles III, IV and V were computed against the hypothesis) a period of  $188 \pm 5$  days for each cycle proved to be significant ( $P < 0.01$ ).

We wondered whether records made by other scientists would fit into the rhythmic pattern we had found, and evaluated the samplings of *Camponotus gigas* reproductives from the Forest Research Institute Sandakan (see Tab. 2). Two samples from Poring lie

TABLE 2. Comparable sampling dates of reproductives from the collection of the Forest Research Institute in Sepilok, District Sandakan, Sabah.

Location	Date	Sex
Lungmanis	6 October 1962	♂
Lungmanis	25 December 1967	♂
Lungmanis	8 November 1968	♂
Silam, Mile 17	6 June 1969	♀
Silam, Mile 17	20 June 1970	♂
Poring, Ranau	11 April 1978	♀
Poring, Ranau	3 May 1980	♂

753 days apart, corresponding to  $4.005 \times 188$  days. The probability of this finding, calculated according to the hypergeometrical distribution, is 0.0013. The two specimens from Silam lie 379 days apart, representing 2.01 periods (probability  $p = 0.0018$ ). Only the samples from Lungmanis are not very clearly synchronized. The older specimens lie 1906 days apart, 26 days longer than would be expected for 10 cycles. Calculating from the oldest to the youngest the result is 11.8 periods of 188 days.

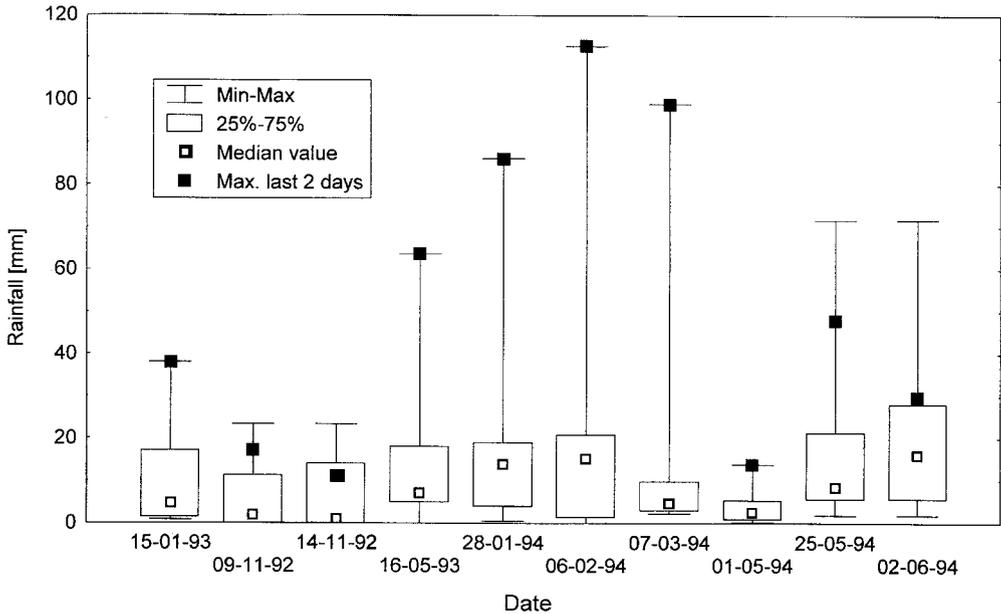


FIG. 2. The whiskers show maxima and minima of the precipitation during the preceding 11 days before nuptial flights. The black square indicates the rainfall maximum during the last two days before the flight. In all cases this maximum is greater than the median of the full period (white square) showing that all flights took place after a short period of relatively heavy rain (see Table 1 for rain data on the day of the flight and the day before).

However, in all these samples the locality is described only roughly, so that these nests may lie far apart. In the headquarters of Kinabalu Park, Mr. Toru Kikuta caught winged *C. gigas* on three occasions: 11 August 1993, 15 November 1993 and 16 May 1994. The interval between the last two flights is 182 days.

## DISCUSSION

The behavioral pattern of the mating flight of the giant ant *C. gigas* is similar to that of the European *Camponotus herculeanus* (Hölldobler & Maschwitz 1965). However, *C. herculeanus* has approximately 50 times more sexuals per flight than *C. gigas*. But the main difference between temperate and tropical species is the timing of reproduction.

In temperate latitudes the reproduction of ants follows an annual cycle. The development of reproductives ends in summer and climatic conditions can trigger swarming within a narrow time-window, e.g., swarming of the *Formica rufa*-group in Germany is triggered by low atmospheric pressure (Klimetzek & Faas 1994). In several species of *Lasius* and *Myrmica*

on the coast of the Netherlands the nuptial flights are triggered by temperature, relative humidity and global radiation (Boomsma & Leusink 1981). In *C. herculeanus* the reproductives swarm several times within a short period in summer (Hölldobler & Wilson 1990).

The dates of the nuptial flights in *C. gigas* in Kinabalu National Park, however, are spread over the whole year. Such a flight behavior was also found in *Paraponera clavata*, the South American "giant ant" (Kannowski 1991). This shows that because of the favorable tropical climate, reproduction is possible during all seasons. Here we present for the first time a detailed analysis of such a flight pattern. The findings from Poring were tested by evaluating flight dates of museum specimens from other sites. The dates when these specimens were collected seem to corroborate our hypothesis rather than to disfavor it: we suggest that the nuptial flight of *C. gigas* occurs with a period of approximately 188 days depending on an circa-semiannual endogenous colony-specific rhythm. The exact date within a narrow time-

window may be triggered by short term climatic events.

Such semiannual cycles are rare, but can be found in the reproductive cycles of tropical birds (Gill 1990) or the sea scallop (Diabacco 1991). However, the mating flight period of *C. gigas* is not exactly semi-annual, it lasted approximately one week longer. Therefore flight times shift over the years. Shifting breeding cycles are also known for two bird species in Sarawak (Fogden 1972) and for other tropical birds (Gwinner 1996).

In the above examples it is likely that reproduction is triggered by an "internal clock" that provides a stable rhythm. Endogenous timing guarantees a better synchronization and less year to year variability than do most environmental factors (Gwinner 1996). For *C. gigas* we observed quite a constant rhythm with a period length of 188 days. This points

towards a strong endogenous component. An endogenous periodicity in egg laying and larval development is described by Kipyarkov (1993, 1994) for several temperate ant species. The reproductive cycle of *Eciton* army ants colonies, that controls their activity cycle, is also endogenous (Schneirla 1971, review in Hölldobler & Wilson 1990).

Endogenous oscillations are controlled by exogenous *zeitgebers* (Palmer 1976). The most reliable clue for the time of year outside the equatorial tropics is the length of the daily photoperiod; another possibility is the measurement of changes in temperature (Page 1985). Both parameters vary only very little near the equator. Here, temperature seems to have no effect on insect seasonality, day length may have some influence (Wolda 1988). However, from 5°N or S of the equator day length differences are too short to trigger the diapause in all studied insect

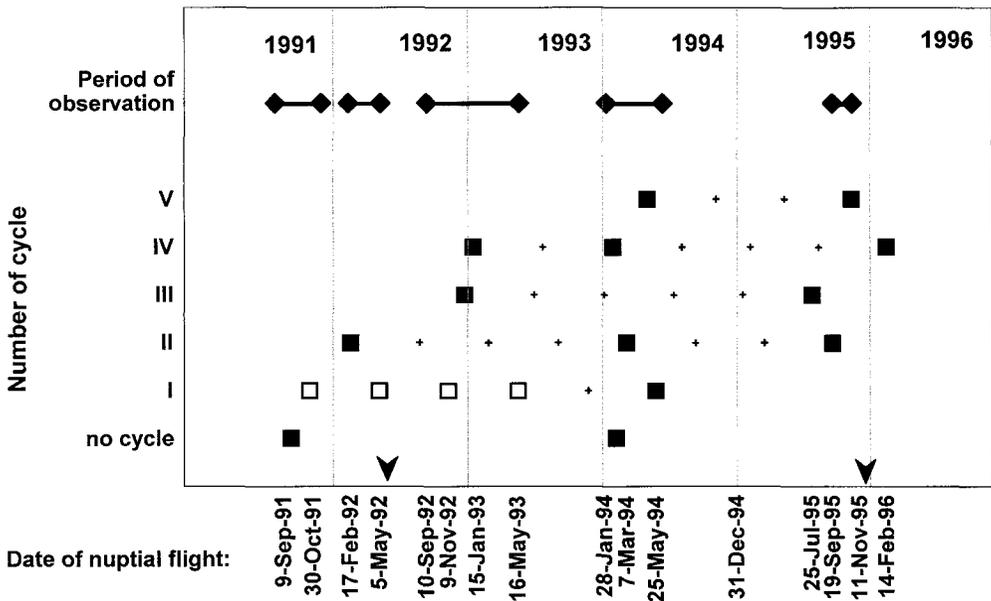


FIG. 3. Nuptial flight rhythm in *Camponotus gigas*. On the X-axis the time of the year is noted, along the y-axis the numbers of the cycles. White squares mark the timing of mating flights observed directly at the main nest K. The black squares mark the timing of nuptial flights observed mostly at artificial lights. Our permanent observation periods are marked by lines connecting black rhombi. (C. Brühl made the observation on 25 July 1994, A. Floren that on 14 February 1996.) We arranged the data to five different cycles with a period length of  $188 \pm 5$  days. Each cycle starts at a different time. Two flights could not be fitted into this pattern (lowest line, for exact data see Table 1). Small crosses mark dates which lay within the rhythm, but with no observation of a nuptial flight. Most of these dates – but not all – lay outside our observation time. Two arrows mark the period of time which was used for the statistical test. The null hypothesis of even distribution could be rejected with 99 % probability (see Methods).

species (Denlinger 1986). A third possible *zeitgeber* is the lunar cycle, and this seems likely to play a role in triggering the giant ants' mating flight, which shows a rather unseasonal pattern. But its influence is not obvious (contrary to e.g., *Clunio marinus*, Neumann 1981) and at present we do not know enough to discuss how it may control the flight synchronization of *C. gigas* colonies. We likewise need more knowledge about the development of the sexuals, for example how long reproductives stay in the nest as adults before flying, before we can ponder how lunar periodicity may influence swarming dates.

Theoretically, a synchronization of the mating flights of *C. gigas* would be possible through a semiannual development cycle of the reproductives with some lunar component. Their swarming could be "fine-tuned" by short-term climatic events (precipitation, atmospheric pressure oscillations). Rainfall seems to have some effects – heavy rainfall at the moment of swarming can stop the departure, while most of the flights followed rather heavy precipitation. In general, however, no prediction of the flight dates can be made using these exogenous parameters. In the continuously warm tropic climate, temperature fluctuations and radiation differences are relatively small and not predictable. The same is true (with reservations) for the distribution of precipitation. The yearly rainfall maxima in Kinabalu Park headquarters (at the upper distribution boundary of *C. gigas*) changed in six out of nine years to a different month (Kitayama 1992). At our observation area in Poring we measured 3218 mm precipitation during 1993, with a minimum of 115 mm in April, thus fulfilling the definition of van Schaik *et al.* (1993) for non-seasonality. This indicates that rainfall can only serve as a trigger that synchronizes the swarming of neighboring colonies within a short period of time. Because of its strong local differences (e.g., Dykes 1994) the equatorial climate may even cause desynchronization in ant colonies co-existing within the range of potential genetic exchange. Yet there must be a mechanism to prevent total asynchrony.

The constant climatic conditions within the aseasonal tropics in Borneo do not require an exact seasonal timing of the reproductive cycle within the geophysical course of the year. This milieu seems to be suited to allow reproduction all the year round. In *C. gigas* we observed semi-annual swarming, shifting breeding cycles and desynchronization. Deviation from a seasonal rhythm and from synchronization within the population may happen if

it leads to reproductive rewards. Such benefits may be gained by a shortening of the reproductive cycle as shown in the examples above. Within the constant climate of a rain forest, unpredictable fluctuations produce short-term stochastic effects. Compared to an annual periodicity a shifting, semi-annual rhythm may multiply the chance of meeting favorable conditions for mating and colony founding, thus reducing the risk of a complete reproductive failure due to adverse environmental conditions within the short period between departure and occupation of a nest site. In *C. gigas*, colony founding is claustral (Pfeiffer 1997). So once she has found a suitable nest site, the queen is relatively independent of such climatic fluctuations.

Ims (1990 a) points out that in a heterogeneous environment, with females that tend to maintain individual territories, the different onsets of triggering cues (e.g., local pattern of rainfall) may produce spatio-temporal patterns of reproduction. Asynchronous reproduction can serve as an anti-predator strategy, especially if prey has a low density and the predator is a generalist switching between alternative prey (Ims 1990 b). For *Camponotus gigas*, with its low number of gynes, a predator swamping is impossible on the population level. Here an asynchronous strategy may be more favorable, perhaps in combination with using the thinning effect of other ant species that often fly on the same days (pers. observation). However, at the colony level all mature sexuals start in the same nuptial flight. We never saw reproductives starting before or after the main flight (with especially the latter behavior being reported for other ant species, Talbot 1945). This strategy seems to fit only species with a high density of colonies or with many small sexuals that fly very well and thus can afford extended search flights. *C. gigas*, however, has huge territories and heavy queens that do not fly well, but seem to be a good prey. Here, this strategy would reduce the chance of finding a mate and should be avoided because of high predation pressure.

The asynchrony of the flight cycles could have severe effects on exogamous mating, possibly leading to a reduced gene flow within the population. However, a splitting of the population could promote outcrossing since it may force pairings between members of more distant colonies. Such strategies are known from a variety of plants, e.g., a beetle-pollinated *Dieffenbachia* using asynchronous flowering within the population to prevent inbreeding (Young 1988). The same is true for most species of figs (*Ficus*),

which flower continuously at the population level. Individual trees, however, have a subannual flowering pattern with a high degree of synchrony in some individuals (lit. in Murawski 1995). This serves as a mechanism to encourage interplant pollen dispersal over long distances.

The circa-semiannual nuptial flight of *Camponotus gigas* points to the differing evolution of mating systems in tropical and temperate species. Little is known about the life history of tropical insects (Wolda 1988); this is true also for tropical ants. Future research on this topic should keep an eye on the reproductive phenology of social insects in the tropics and on the mechanisms that ensure synchronization and outbreeding in an environment where life is not fixed to a rigid pattern of seasonality.

### ACKNOWLEDGEMENTS

We are grateful to Sabah Parks for the assistance and help that allowed this study to be conducted. We thank especially Daruk Dr. Lamri Ali, Mr. Francis Liew, Mr. Rajibi Hj. Aman, Mr. Eric Wong, Mr. Jamili Nais and Mr. Kasitah Karim for various kinds of support. With the help of many members of the "German Research Team" in Poring we were able to observe almost continuously. Special thanks to Holger Wittekindt, Armin Götzke, Carsten Brühl, Dr. Andreas Floren and Jan Beck. Further thanks are due to the curator of the Forest Research Institute, Sandakan, Mr. Chung and to Mr. Toru Kikuta, who collected specimens for the Kinabalu Museum. We thank Prof. Dr. Herbert Vogt for his mathematical advice, Prof. Dr. Konrad Fiedler and our two reviewers Prof. Dr. Hölldobler and Prof. Dr. Kannonowski for helpful comments on the manuscript, Dr. Ulmar Grafe and Dr. David Proudler for improving the English, and Walter Jetz for tips to the literature. This study was supported by the "Deutscher Akademischer Auslandsdienst" (DAAD), Bonn. We also thank the "Deutsche Forschungsgemeinschaft" (DFG) for granting the infrastructure for our activities within the framework of the "DFG Schwerpunktprogramm Mechanismen der Aufrechterhaltung tropischer Diversität."

### REFERENCES

- Ashton, P.S., Givnish, T.J., & S. Appanah. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *Am. Nat.* 132: 44–66.
- Boomsma, J.J., & A. Leusink. 1981. Weather conditions during nuptial flights of four European ant species. *Oecologia* 50: 236–241.
- Chung, A.Y.C., & M. Mohamed. 1993. The organisation and some ecological aspects of the giant forest ant, *Camponotus gigas*. *Sabah Society Journal* 10: 41–55.
- Denlinger, D.L. 1986. Dormancy in tropical insects. *Ann. Rev. Entomol.* 31: 239–264.
- Diabacco, C. 1991. Considering a semiannual reproductive cycle for the sea scallop *Placopecten magellanicus* on Georges Bank. *J. Shellfish Res.* 10: 271–272.
- Dykes, A.P. 1994. Rainstorm patterns. Pp. 24–25 in Cranbrook, E.O., & D.S. Edwards (eds.). *A tropical rainforest – the nature of biodiversity in Borneo at Belalong, Brunei*. London.
- Floren, A., & K.E. Linsenmair. 1994. Zur Diversität und Wiederbesiedlungsdynamik von Arthropoden auf drei Baumarten in einem Regenwald in Sabah, Malaysia. *Andrias* 13: 23–29.
- Fogden, M.P.L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* 114: 307–343.
- Gault, D. 1987. Feeding and foraging behaviour of the Giant Forest Ant, *Camponotus gigas*, in a Malaysian rain forest. *Tropical Biology Newsletter* 52: 2.
- Gill, F.B. (ed.). 1990. *Ornithology*. New York.
- Gwinner, E. 1986. Circannual rhythms. Heidelberg.
- Gwinner, E. 1996. Circannual clocks in avian reproduction and migration. *Ibis* 138: 47–63.
- Hartley, R., & K. Husler. 1993. A less-than-annual breeding cycle in a pair of African Bat Hawks *Machaeramphus alcinus*. *Ibis* 135: 456–458.
- Hölldobler, B., & U. Maschwitz. 1965. Der Hochzeitschwarm der Rossameise *Camponotus herculeanus* L. (Hym. Formicidae). *Z. vgl. Physiol.* 50: 551–568.
- Hölldobler, B., & E.O. Wilson. 1990. *The ants*. Cambridge, Mass.
- Ims, R.A. 1990 a. The ecology and evolution of reproductive synchrony. *TREE* 5: 135–140.
- Ims, R.A. 1990 b. On the adaptive value of reproductive synchrony as a predator-swamping strategy. *Am. Nat.* 136: 485–498.
- Inger, R.F., & J.P.J. Bacon. 1968. Annual reproduction and clutch size in rain forest frogs from Sarawak. *Copeia* 68: 602–6.
- Inger, R.F., & B. Greenberg. 1967. Annual reproductive patterns of lizards from a Bornean rain forest. *Ecology* 47: 1007–1021.
- Janzen, D.H. 1976. Why Bamboos wait so long to flower. *Ann. Rev. Ecol. Syst.* 7: 347–391.
- Kannonowski, P.B. 1991. Occurrence of alates of the neotropical ant, *Paraponera clavata* (Hymenoptera, Formicidae), at lights during the dry-wet seasons interface in Panama. *J. Entomol. Sci.* 26: 375–377.

- Kelly, D. 1994. The evolutionary ecology of mast seeding. *TREE* 9: 465–470.
- Kipyatkov, V.E. 1993. Annual cycles of development in ants: diversity, evolution, regulation. Pp. 25–48 in Kipyatkov (ed.). Proceedings of the colloquia on social insects. St. Petersburg.
- Kipyatkov, V.E. 1994. The role of endogenous rhythms in the regulation of annual cycles of development in ants (Hymenoptera, Formicidae). [In Russian with Engl. summary]. *Entomol. Obozr.* 73: 540–553.
- Kitayama, K. 1992. An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio* 102: 149–171.
- Klimetzek, D., & G. Faas. 1994. Influence of weather and nest site on the nuptial flight of hill-building wood-ants of the *Formica rufa*-group (Hym. Form.). *J. Appl. Ent.* 117: 508–518.
- Medway, F.L.S.L. 1972. Phenology of a tropical rain forest in Malaya. *Biol. J. Linn. Soc.* 4: 117–146.
- Müller, H.J. 1992. Dormanz bei Arthropoden. Jena.
- Murawski, D.A. 1995. Reproductive biology and genetics of tropical trees from a canopy perspective. Pp. 457–492 in Lowman, M.D., & Nadkarni, N.M. (eds.). *Forest Canopies*. San Diego.
- Neumann, D. 1981. Tidal and lunar rhythms. Pp. 351–380 in Aschoff (ed.). *Biological Rhythms. Handbook of behavioral neurobiology*. Vol. 4. New York.
- O'Brian, G.M. 1993. Seasonal reproduction in flying foxes, reviewed in the context of other tropical mammals. *Reproduction Fertility and Development* 5: 499–521.
- Orr, A.G., & J.K. Charles. 1994. Foraging in the giant forest ant, *Camponotus gigas* (Smith) (Hymenoptera: Formicidae): evidence for temporal and spatial specialisation in foraging activity. *J. Nat. Hist.* 28: 861–872.
- Page, T.L. 1985. Clocks and circadian rhythms. Pp. 577–652 in Kerkut, & Gilbert (eds.). *Comprehensive insect physiology, biochemistry and pharmacology*. New York.
- Palmer, J.D. 1976. *An introduction to biological rhythms*. New York.
- Pfeiffer, M. 1997. Sozialstruktur und Verhaltensökologie von Riesenameisen *Camponotus gigas* Latreille 1802 im Regenwald Malaysias auf Borneo. PhD Thesis Universität Würzburg. Berlin.
- Schneirla, T.C. 1971. *Army ants: a study in social organization*. San Francisco.
- Sokal, R.R., & F.J. Rohlf. 1995. *Biometry – the principles and practice of statistics in biological research*. Third edition. New York.
- Talbot, M. 1945. A comparison of flights of four species of ants. *Am. Midl. Nat.* 34: 504–510.
- Tobin, J.E. 1995. Ecology and diversity of tropical forest canopy ants. Pp. 129–147 in Lowman, M.D., & N.M. Nadkarni, (eds.). *Forest canopies*. San Diego.
- van Schaik, C.P., Terborgh, J.W., & S.J. Wright. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Ann. Rev. Ecol. Sys.* 24: 353–377.
- Wells, D.R. 1976. Resident birds. Chapter 1 in Medway, F.L.S.L., & D.R. Wells (eds.). *Birds of the Malay Peninsula*. London.
- Whitmore, T.C. 1988. *Tropical rain forests of the far east*. Second edition. Oxford.
- Whitmore, T.C. 1990. *An introduction to tropical rain forests*. Oxford.
- Wilson, E.O. 1975. *Sociobiology: the new synthesis*. Cambridge, MA.
- Wilson, E.O. 1987. The arboreal ant fauna of Peruvian Amazon forests: a first assessment. *Biotropica* 19: 245–251.
- Wolda, H. 1988. Insect seasonality: why? *Ann. Rev. Ecol. Syst.* 19: 1–18.
- Wright, S.J., & O. Calderon. 1995. Phylogenetic patterns among tropical flowering phenologies. *J. Ecology* 83: 937–948.
- Wright, S.J., & C.P. van Schaik. 1994. Light and the phenology of tropical trees. *Am. Nat.* 43: 192–199.
- Young, H.J. 1988. Neighborhood size in a beetle pollinated tropical aroid: effects of low density and asynchronous flowering. *Oecologia* 76: 461–466.