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Various population fluctuation patterns of light-attracted beetles in a tropical lowland dipterocarp forest in Sarawak

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Abstract The population fluctuation pattern of light-attracted beetles was studied from August 1992 to September 1998 (for 73 months) using ultraviolet light-traps set at three vertical levels in a tropical lowland dipterocarp forest in Sarawak, Malaysia. During our study, a general flowering occurred from April to July in 1996, and flowering on a small scale in 1997 and 1998. We analyzed the data for eight scarabaeid and six meloid species, some of which were anthophilous species. Various fluctuation patterns were observed among the beetle species in aspects of both seasonality and correlation with the supraannual phenological pattern. Three large chafer species (Scarabaeidae, Melolonthini) showed a clear seasonal fluctuation pattern with a peak once from March to May every year, the peak monthly catch greatly fluctuating annually. Other scarabaeid beetles did not show such a clear seasonal population pattern and hardly fluctuated annually. Populations of an anthophilous scarabaeid species, *Parastasia bimaculata*, a specific pollinator of *Homalomena propinqua* (Araceae), hardly fluctuated, probably because of its response to the constant flowering of its floral hosts. Monthly catches of an anthophilous scarabaeid, *Anomala* sp., and meloid beetles showed clear supraannual patterns in response to the general flowering and were significantly correlated with the flowering intensity with or without a lag of a month. The fluctuation pattern of meloids suggests a supraannual population fluctuation pattern of their hosts, i.e., megachilid/anthophorid bees.

Key words General flowering · Light-trap · Population dynamics · Scarabaeidae · Meloidae · Borneo

Introduction

Although seasonal changes in temperature tend to be minimal or absent in the tropics, an alternation between a drier and a wetter season is apparent in many areas. In such weakly seasonal tropical forests, flowering phenology and insect population dynamics have seasonal patterns. For example, in forests in the Neotropics, various types of seasonality patterns of population dynamics can be found in tropical insects (Wolda 1978, 1988, 1998).

In contrast, in the wettest parts of Southeast Asia, such an alternation between a drier and a wetter season is inconspicuous, and it is constantly humid throughout the year (Whitmore 1984; Inoue and Nakamura 1990). In addition to seasonality, recurrent climatic changes occur at 4- to 5-year intervals (El Niño-Southern Oscillation, ENSO) (Inoue et al. 1993). Most forest canopy tree species, including many dipterocarps, are triggered to mass-flower under unusually cool dry weather conditions in El Niño years (Ashton 1991; Yap and Chan 1990; Appanah 1993) or under cool cloudy weather conditions in La Niña years (Sakai et al. 1999a,b) in response to ENSO. It is not yet known how arthropod populations in the dipterocarp forests fluctuate under these weakly seasonal and annually unpredictable conditions and in response to the long-term climatic oscillations. Because the general flowering is a drastic event in that many canopy tree species mass-flower within a few months at supraannual intervals, it may affect population dynamics of arthropods which have associations with flowers or fruits of these trees more clearly than seasonal events.

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Light-trapping is a method useful for monitoring general temporal trends of insect abundance. Analyses of long-term light-trap data in the Neotropical forests where wet and dry seasons alternate have provided evidence that tropical insects undergo seasonal changes in abundance and that the seasonal fluctuation patterns are diverse and different among species and among feeding habits (Wolda 1978, 1980, 1988, 1998).

In a lowland dipterocarp forest in Lambir Hills National Park, Sarawak, we have been surveying the phenology of flowering, fruiting and flushing of canopy trees since 1992 (Momose et al. 1998; Sakai et al. 1999b) and have been continuing a light-trap census of night-flying insects (Kato et al. 1995). The objective of this article is to describe population fluctuation patterns of the light-attracted insects in the dipterocarp forest and to test the hypothesis that the fluctuation patterns are affected by the supraannual flowering phenology patterns. The insect taxa that we analyzed for their population fluctuations were abundant species of two coleopterous families, Scarabaeidae and Meloidae; some species of the former family and all the latter have flower-visiting habits.

Here, (1) we examined the temporal patterns of flowering and fruiting of plants for 6 years, (2) analyzed the temporal patterns of light-trapped populations of several scarabaeid and meloid beetle species and tested the presence or absence of seasonality among them, and (3) investigated the correlations of monthly insect catches with percentages of flowering and fruiting plant individuals and with monthly rainfall. Finally, we discuss the seasonal, annual, and supraannual temporal patterns of light-trapped insect abundance in the supraannually oscillating climate.

Materials and methods

The study site was Lambir Hills National Park, Miri, Sarawak, Malaysia (4°2′N, 113°50′E, altitude 120–250m above sea level). The park is located about 10km inland from the coast in the northern part of Sarawak, and the climate is humid tropical with a weak seasonal change in rainfall (Fig. 1). Most of the park is covered with primary evergreen forests, much of which is classified as lowland mixed dipterocarp forest formed on nutrient-poor sandy or clayey soil (Ashton 1991). The forest is multilayered and the canopy is about 35–40m high. Emergent trees penetrating the canopy layer can attain heights of more than 70m.

Flowering and fruiting phenology were observed in the Canopy Biology Plot (8ha, 200 × 400m) and a belt transect along the waterfall trail (5ha, 1km × 50m) (Sakai 1999b). At the center of the Canopy Biology Plot, a canopy observation system composed of two tree towers (T1 and T2), nine aerial walkways, and seven tree terraces was constructed (Yumoto et al. 1996). The heights of T1 and T2 are 33m and 48m, respectively, and the walkways penetrated the canopy or subcanopy layer. The waterfall trail is located along a stream on yellow sandstone, from the headquarters of the park to the Operation Raleigh Tower, which is another tree tower constructed by Operation Raleigh and donated to the park. Percentages of flowering and fruiting plant individuals at each census date were obtained and defined as flowering and fruiting intensities, respectively.

Air temperature, rainfall, illumination, and relative humidity were all measured at the 35-m level on the tree tower (T1) from January 1992 and additionally at the 17- and 1-m levels from May 1992 (Yumoto et al. 1996). Flowering and fruiting of 576 individual plants of 305 species in 56 families were monitored from the tree towers and walkways twice a month, and/or from the forest floor once a month from August 1992 (Sakai et al. 1999b).

Light-trap collections have been made at various levels on the tree tower (T1) from August 1992 to March 1999 (data from September 1997 to March 1998 missing) using modified Pennsylvania ultraviolet light-traps consisting of a 20-W mercury vapor lamp, two crossed transparent boards for intercepting light-attracted flying insects and a bucket to receive the fallen insects. Nocturnal flying insects, attracted

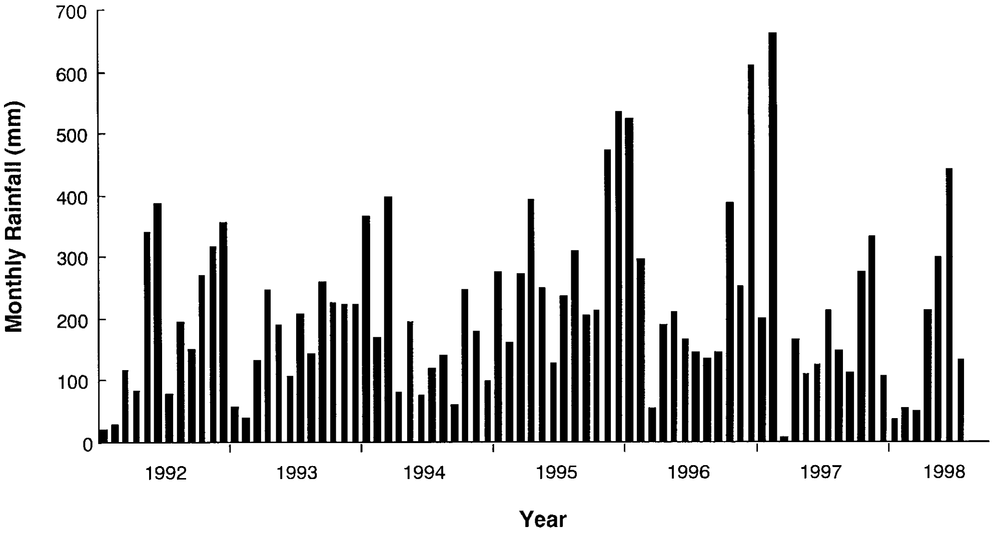


Fig. 1. Fluctuations of monthly rainfall (mm) at Lambir National Hills park in Sarawak

to a light, hit the boards below the light and fell into a bucket filled with 50% ethanol. Three light-traps were set on platforms at the 1-, 17-, and 35-m levels of the tree tower. To restrict light throw to specific vertical layers, upward and downward light throw was cut by the platform. The light-traps were set up throughout the night over four (August 1992 to August 1993 and from April 1998 to September 1998) or six (from September 1996 to August 1997) consecutive nights around the period of new moon. We analyzed the data from August 1992 to September 1998 (samples at 1- and 17-m levels were available only from February to July 1993).

The trapped insect specimens were recovered from the buckets every morning. Larger specimens (~>7 mm) and all coleopterans (after September 1993) were pinned and dried in a drying box under 100-W incandescent lamps. All pinned specimens were labeled and sorted by insect order. Collections containing numerous smaller insects such as chalcid wasps were sorted by orders and preserved separately in vials filled with 70% ethanol. All insect specimens are preserved at the Forest Research Center in Kuching, Sarawak. Seasonal fluctuations of all insect groups from August 1992 to August 1993 are reported by Kato et al. (1995).

Insect species analyzed for dynamics involve eight scarabaeid and six meloid beetle species (Table 1), which were medium-sized to large insects with relatively great abundance. Meloid species, all of which belonged to the genus *Zonitis*, were treated as a group. Individual numbers of these species trapped for each trapping sequence were counted, and the monthly catch was estimated as the daily mean of the total numbers trapped at three vertical levels per night. Among the scarabaeids, *Hoplia aurata*, *Anomala* sp., and *Mimela maculicollis* are known to be visitors of various flowers and *Parastasia bimaculata* to visit flowers of *Homalomena propinqua* (Araceae) (Kato 1996). Numbers of these trapped insects per night at the 1-, 17-, and 35-m levels from August 1992 to September 1998 were then analyzed.

Results

During our phenology study from 1992 to 1998, general flowering occurred four times: from March to May in 1992 (quantitative data are lacking), from March to September in 1996, from March to May in 1997, and from March to June 1998 (Fig. 2). Among 428 plants that had been monitored for flowering and fruiting from the walkway system (237 species, excluding *Ficus* and forest floor plants), percentages of flowering plants, i.e., flowering intensities, were maintained at less than 4% from April 1993 to February 1996.

Abrupt decreases in daily minimum temperature to below 19.5°C were observed on February 3 and March 4 in 1996 and January 2–4 in 1997. The two events of low temperature in 1996 preceded the two peaks of general flowering in 1996. The meteorological data from October 1997 to January 1998 are lacking, during which time daily minimum temperature might have decreased below 19.5°C.

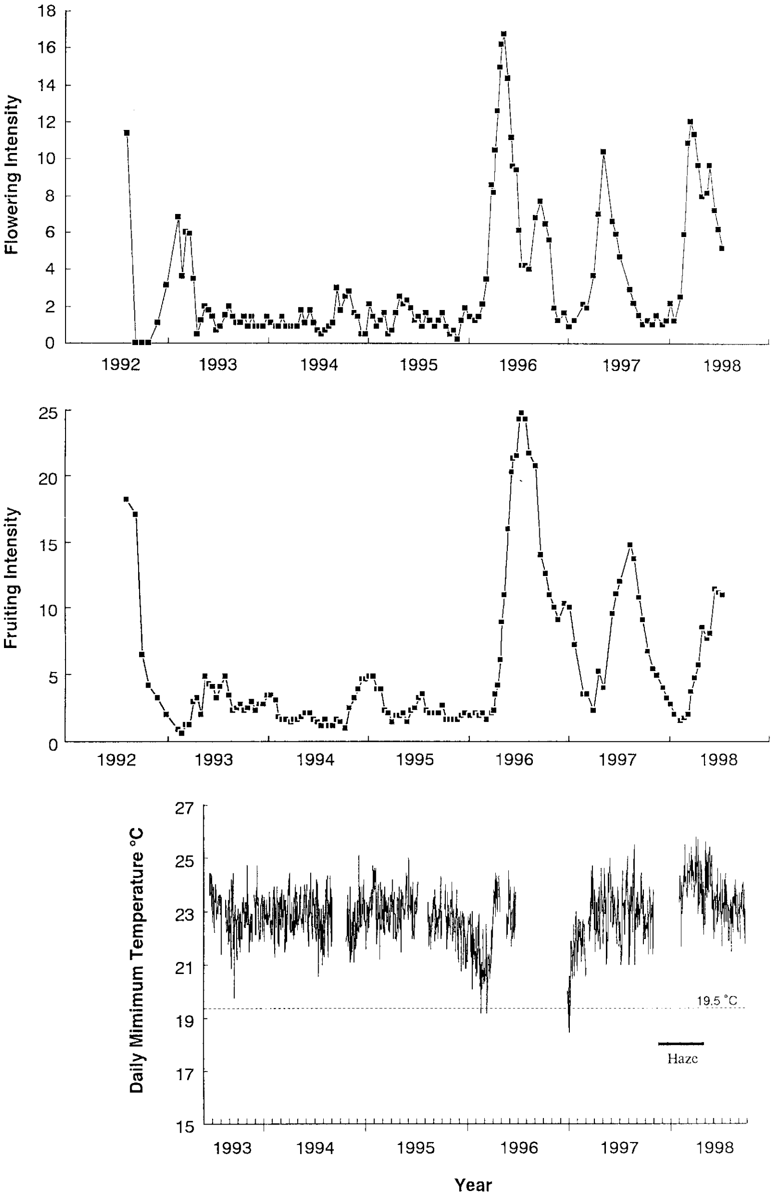
Extraordinary drought caused by a strong El Ninõ started in 1997 in Southeast Asia, and extensive fires started to occur in Sarawak in July 1997. The forest in Lambir was covered by haze that was produced by the fires. The daily minimum temperature was kept at a higher level from February to May 1988 when nearby forests were burning (Fig. 2).

During our 6-year light-trap census, 7243 scarabaeid and 621 meloid beetles were collected by light-trapping (Table

Table 1. A list of the beetle species whose population fluctuations were monitored by light-trapping, and their total light-trap catches, flower-visiting habit, and floral host species recorded in Lambir Hills National Park

Family Subfamily Tribe Species	Total catches	Flower-visiting habit	Floral hosts recorded
Scarabaeidae			
Melolonthinae			
Melolonthini			
Asactopholis pectoralis Mos.	4312	Absent	
Asactopholis sp.	739	Absent	
Psilophoris vestita (Sharp)	1268	Absent	
Hoplini			
Hoplia aurata Waterhouse	500	Present	*Shorea parvifolia*
Rutelinae			
Anomalini			
Anomala sp.	80	Present	*Shorea* spp., *Vatica micrantha, Hopea philipinensis, Croton* sp., *Drypetes* sp.
Mimela maculicollis Ohaus	50	Present	*Shorea parvifolia*
Parastasiini			
Parastasia bimaculata Guerin	183	Present	*Homalomena propinqua*
P. confluens Westw.	111	Unknown	Unknown
Meloidae			
Zonitinae			
Zonitis spp.	621	Present	Unknown

Fig. 2. Changes in flowering (*top*) and fruiting (*middle*) intensities and in daily minimum temperature (*bottom*) at Lambir Hills National Park in Sarawak



1). A comparison of the mean monthly catches of each beetle species among the three vertical levels (Fig. 3) revealed that the catch tended to increase along the vertical levels in four scarabaeid species and in meloids. Decreasing trends of catches along vertical levels were detected in two scarabaeid species, *Anomala* sp. and *Parastasia bimaculata*.

Among the studied beetle species, five scarabaeid and two meloid species visited the flowers (see Table 1). *Parastasia bimaculata* visited specifically *Homalomena propinqua* (Araceae) flowers almost throughout the year. In the spathe of the aroid, a pair of these beetles were observed to be staying or copulating.

Monthly light-trap catches of eight scarabaeid beetle species fluctuated greatly during the 6 years (Fig. 4). Three melolonthine species, *Asactopholis pectoralis*, *Asactopholis* sp., and *Psilophoris vestita*, showed clear seasonality, suggesting their annual life cycles. Their monthly catches peaked from March to May every year and were nearly zero during the other months. We calculated autocorrelations in monthly catches of these beetle species and detected significant annual autocorrelations (Fig. 5). The annual peak of the catches fluctuated from year to year, and the magnitudes of fluctuation, i.e., the ratios of maximum to minimum peak catch of *A. pectoralis*, *Asactopholis* sp., and *P. vestita* were about 300, 200, and 20, respectively. The other five scarabaeid species did not show clear seasonal fluctuation patterns.

The fluctuations of the eight scarabaeid species were not significantly correlated with the flowering intensity, fruiting intensity, or monthly rainfall, except in an anthophilous scarabaeid, *Anomala* sp., whose population dynamics was significantly correlated with flowering intensity, and except in *Parastasia bimaculata*, whose population dynamics was significantly correlated with fruiting intensity (Table 2).

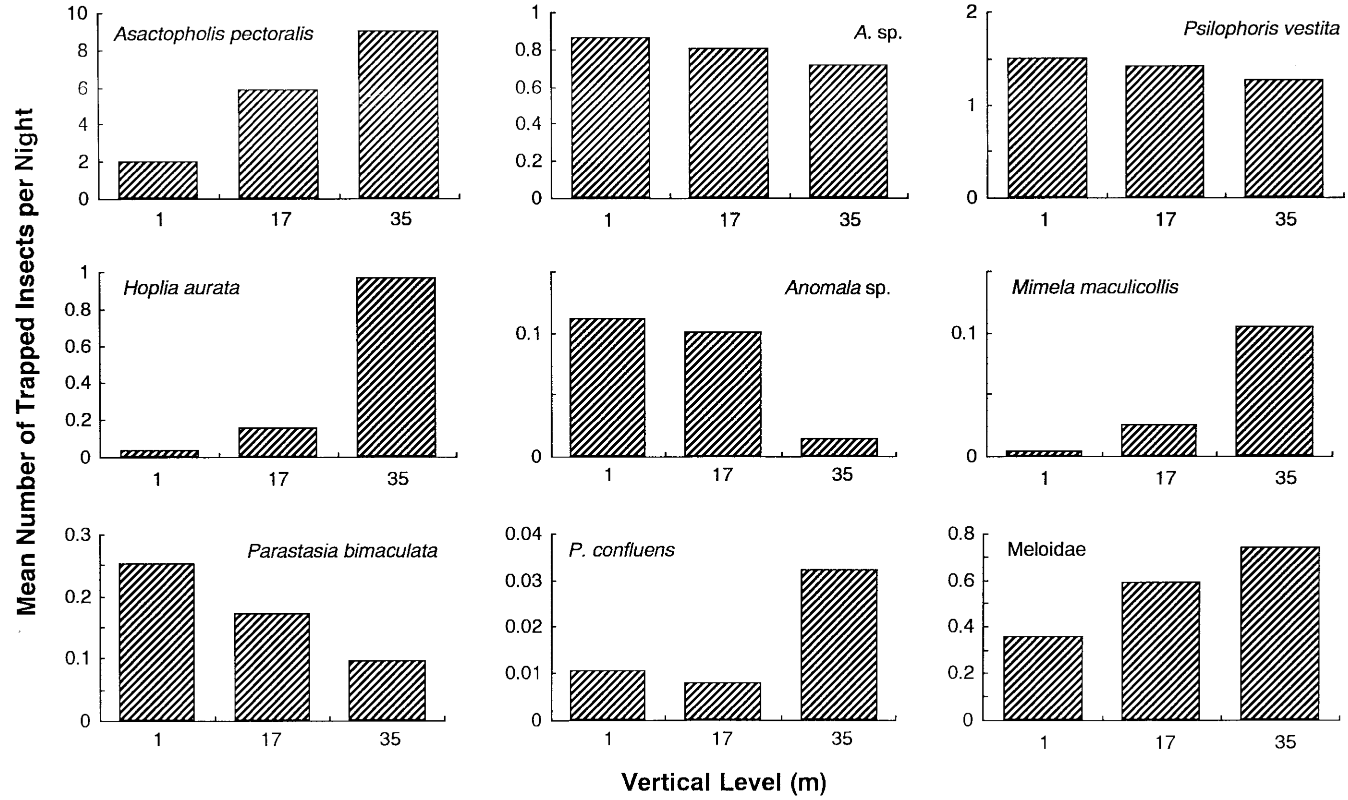


Fig. 3. Vertical distributions of the mean monthly catches (from February 1993 to September 1998) for nine taxa of beetles

Table 2. Significance of correlations of monthly catches against flowering and fruiting intensities and rainfall with lags of 0 to 3-month

Family Species	Variables											
	Flowering intensity				Fruiting intensity				Rainfall			
	t	t-1	t-2	t-3	t	t-1	t-2	t-3	t	t-1	t-2	t-3
Scarabaeidae												
Asactopholis pectoralis	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Asactopholis sp.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Psilophoris vestita	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Hoplia aurata	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.0213	0.0072	n.s.	n.s.	n.s.	n.s.
Anomala sp.	0.0345	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.0321	n.s.	n.s.	n.s.	n.s.
Mimela maculicollis	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Parastasia bimaculata	n.s.	n.s.	0.008	0.0006	0.0089	0.0028	0.0008	0.0102	n.s.	n.s.	n.s.	n.s.
P. confluens	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Meloidae												
Zonitis spp.	0.0001	0.0027	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Numericals denote the probabilities; n.s., non significant

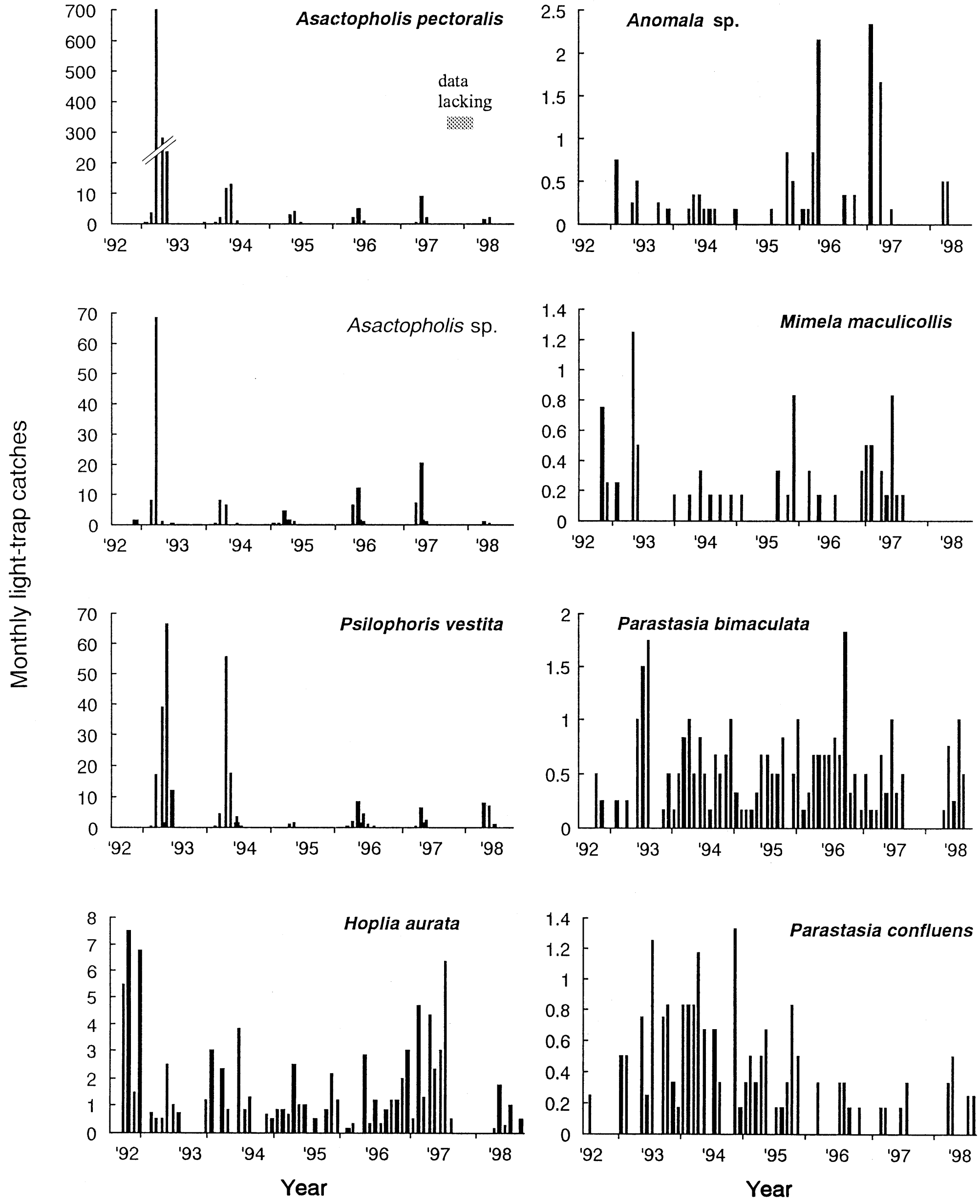
Significant correlations were observed between monthly catches of some anthophilous scarabaeids and the flowering and fruiting intensities 1–3 months earlier. Delayed, significant positive correlations were observed between the monthly catch and preceding flowering and/or fruiting intensities 2–3 months earlier in *Hoplia aurata*, *Anomala* sp., and *Parastasia bimaculata* (Table 2). No significant correlations were observed between monthly catch and rainfall.

Monthly catches of meloid beetles peaked during the flowering period in 1996 (Fig. 6). The population dynamics was not significantly correlated with monthly rainfall and fruiting intensity, but was significantly correlated with the flowering intensity (Table 2). A delayed, significantly positive correlation between monthly catch and 1-month preceding flowering intensity was also detected.

Discussion

This is the first study on long-term insect population dynamics in Bornean dipterocarp forests where general flowering

Fig. 4. Fluctuations of monthly light-trap catches of eight scarabaeid species during 73 months from August 1992 to September 1998



occurs at an interval of 4–5 years. Our data demonstrate that there are various fluctuation patterns among beetle species in aspects of both seasonality and correlation with the supraannual phenological pattern.

At our study site in Sarawak, the daily mean temperature is constantly high throughout the year, and alternation between wet and dry seasons is minimal. However, among eight scarabaeid beetle species collected in light-traps, three melolonthine chafer species showed clear seasonality. The seasonal pattern, first reported by Kato et al. (1995), was supported by this 6-year study. Larvae of most melolonthine chafers are root feeders (Ritcher 1957) and are known to emerge in response to rainfall (Kalshoven 1981; Gaylor and Frankie 1979; Potter 1981; Hilje 1996). Because the seasonality in rainfall pattern was not apparent at the study site (Fig. 1), the environmental factor adopted as the seasonal cue for these chafers may be a factor other than rainfall, as discussed by Wolda (1989).

Generation cycles with discrete populations, however, are common in pest species in the tropics (Perera et al. 1988). In these cases, natural enemies are an important cause of mortality and have been thought responsible for driving the cycle (Godfray and Hassell 1987, 1989). It is still unknown which factors, environmental or internal (e.g., mortalities by natural enemies), caused the observed generation cycles of these three chafer species. In other beetle species that are thought to be multivoltine, no generation cycles were observed, which means that the mortality by specific natural enemies was not important in these tropical forest beetles.

During our study from 1992 to 1998, general flowering occurred four times, i.e., in 1992, 1996, 1997, and 1998,

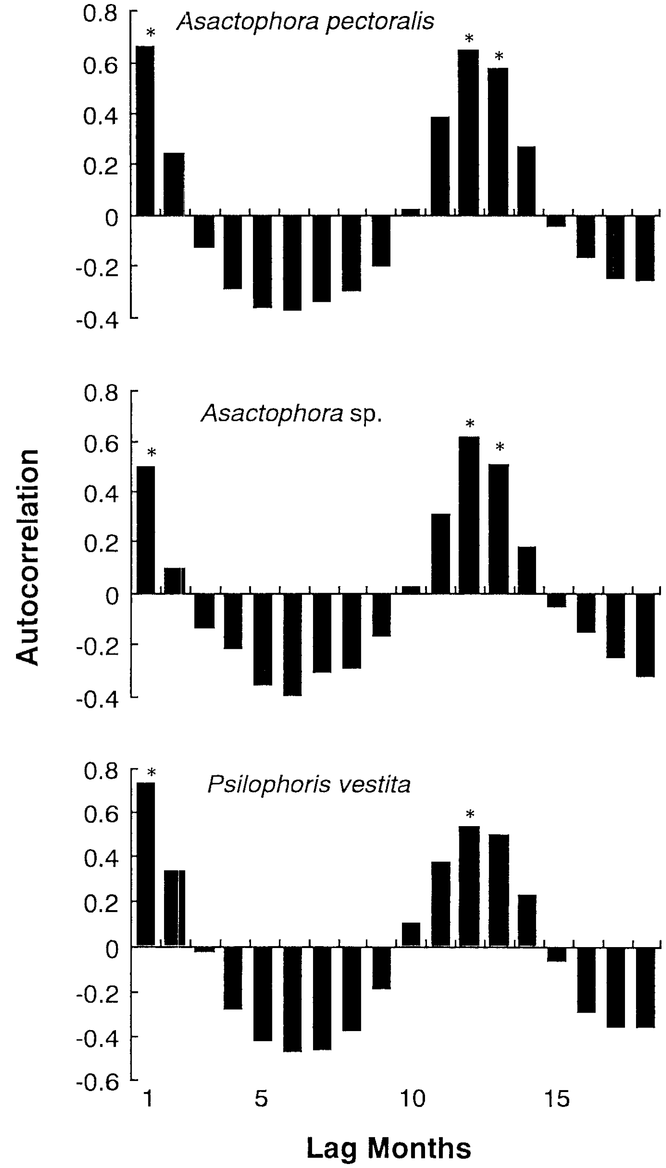


Fig. 5. Autocorrelations in monthly catches of three melolonthine species. *Asterisks* show significant autocorrelations ($P < 0.05$)

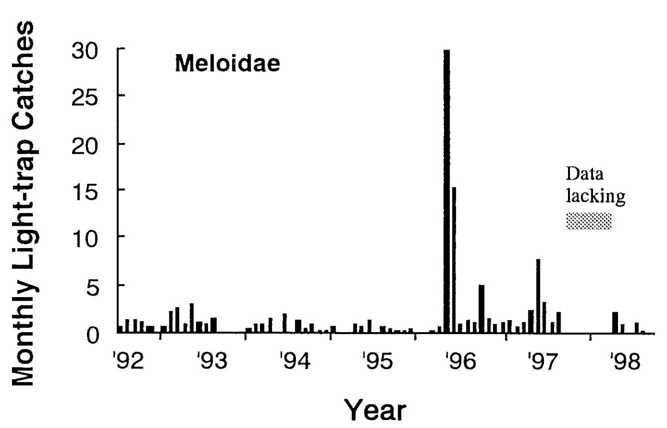


Fig. 6. Fluctuation of monthly light-trap catch of meloid beetles during 73 months from August 1992 to September 1998

whereas the scale of flowering in 1997 and 1998 was small. In this forest where floral resource fluctuated supraannually (see Fig. 2), populations of some beetle groups fluctuated in response to the general flowering. Population fluctuation of an anthophilous scarabaeid species, *Anomala* sp., had significant correlations with the flowering intensity, i.e., the resource level for the beetle. Because adults of some *Anomala* species are pollen feeders while their larvae are plant root feeders, the population level of the sacarabaeid might have been regulated by the floral resource at the adult stage. Different species in the genus *Anomala* differ in habitat, life cycle, anthophilous behavior, and fluctuation pattern. For example, a Neotropical species in Mexico, *Anomala flavipennis*, is a pest of various crops, lacking anthophilous behavior and having a bivoltine life cycle, and its annual fluctuation pattern corresponds to the rainfall and irrigation (Rodriguez-del-Bosque 1998).

Another anthophilous scarabaeid, *Hoplia aurata*, showed a similar fluctuation pattern peaking during the flowering period, while its correlation with flowering intensity was not significant. Although only one plant species (*Shorea parvifolia*) was recorded as its floral host (see Table 1), its possible floral hosts may not be so restricted. It is still unknown whether they utilize rare flowers except during the general flowering period.

Two *Parastasia* species showed a relatively stable, nonseasonal fluctuation pattern. The only floral host species of *Parastasia bimaculata*, *Homalomena propinqua* (Araceae), is a forest-floor herb that blooms haphazardly throughout the year. Because each spathe of plant was observed to be occupied by a pair of scarabaeid beetles and utilized as a mating site, the relatively stable population level of the scarabaeid might be caused by the level of flower abundance of its floral hosts. Because the beetle population had significant correlations with the flowering intensity 2–3 months earlier (see Table 2), the flower abundance of the aroids might have increased during the general flowering period. The population of another syngeneric species, *Parastasia confluens*, fluctuated roughly in inverse relation to the flowering intensity (see Figs. 2, 4). The floral hosts of this scarabaeid are still unknown, and this interesting fluctuation pattern has yet to be explained.

The most clear correlation with flowering intensity was found in the population dynamics of meloid beetles. Larvae of meloids are cleptoparasitoids of megachilid and anthophorid bees. The high population level of meloids during the flowering period in 1996 is thought to result from the high population level of their host bees. The monthly catch of meloids was significantly correlated with the flowering intensity 0–1 months earlier. This lag is thought to be the larval growth period of bees and meloid beetles.

The drought and extensive fires from July 1997 to April 1998 were unusual and severe. Even in the primary forest, not a few canopy trees were killed by the drought. Populations of some scarabaeid species such as *Asactopholis* spp. and *Mimela maculicollis* declined after the drought, whereas other species were not influenced. The impact of the drought upon insect population dynamics should be monitored for a longer period.

There are few detailed studies on insect population dynamics in tropical areas. A phytophagous lady beetle species, *Epilachna vigintioctopunctata*, is a rare example in which long-term density fluctuations and life tables were studied (Abbas and Nakamura 1985; Nakamura et al. 1988, 1990). This species is a pest of a semicultivated shrub, *Solanum torvum*, and its major mortalities were parasitism by eulophid wasps on eggs and pupae and food depletion caused by defoliation by larvae. The lady beetle had eight separate generations per year; populations of immature stages fluctuated with a 48-day cycle. Irrespective of the discrete generations of immature stages, adult populations changed in a gradual process peaking once a year. These studies suggest that even in aseasonal tropical areas a seasonal (or cyclic) fluctuation pattern appears in multivoltine species whose larvae have discrete generations. Royama (1977) suggested that second-order processes characterized by time lags arising from the impact of one generation on the reproduction and survival of the next or later generation result in cyclic behavior. The second-order factors of the lady beetle may be the high mortality caused by parasitoids. In the multivoltine beetle species of our study, cyclic fluctuation patterns were not observed. This result suggests that second-order factors determining cyclic oscillations (e.g., attack by specific parasitoids or parasites) were absent or weak in these tropical forest beetles, which reminds us of the trend that specialist parasitoids decline in frequency toward the tropics as predicted by the resource fragmentation hypothesis (Gauld 1986).

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