

Population dynamics of animals in unpredictably-changing tropical environments

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Abstract. We studied population dynamics of a solitary phytophagous beetle, *Epilachna vigintioctopunctata* and a social stingless bee, *Trigona minangkabau*, in Sumatra, Indonesia for 5 years from 1981.

Population increase of *Epilachna vigintioctopunctata* was suppressed in months of normal rainfall (≥ 300 mm) but was released in the 1982-1983 El Nino-Southern Oscillation when rainfall dropped to 50% of the long-term average. Mechanisms might be direct; rainfall lowered egg hatchability and the time of adult's residence on host plants. When dry weather continued for more than three generations, the *Epilachna vigintioctopunctata* population reached a density at which food shortage due to defoliation occurred. Although parasitism of immature stages was high, it was not a population-regulating factor. Thus, there were two types of ecological crunch: competition for food resources at the end of favourable dry periods and high mortality during heavy rainfall periods that usually followed El Nino-Southern Oscillation dry conditions.

By an experimental addition of artificial nest sites, colony density of *Trigona minangkabau* increased 2.5 times the original density of natural colonies. One-half of artificial nest sites were occupied by arboreal ants and thus competition for nest sites with ants suppressed further increase of *Trigona minangkabau*. Intermediate rainfall was favourable for *Trigona minangkabau* because the rate of colony foundation decreased both during dry El Nino-Southern Oscillation months and months with heavy rain. Colony death was independent from rainfall. Many colonies that survived for 6 months persisted for >2 years and colony density was quite stable. *Trigona minangkabau* colonies could survive even under unfavourable periods, by hoarding resources in the nest. There was no significant ecological crunch during the study period and colony density almost always tracked the carrying capacity of the habitat, which was basically determined by nest-site abundance.

Climatic conditions, especially rainfall, changed with various periodicities, 4-5 years for El Nino-Southern Oscillation, and 2 years for the monsoon and other shorter periods. The contribution of periodicities of 1 and 0.5 years, that were linked to movement of the sun, were weak, indicating that animals could not use seasonal changes of environments, e.g. daylength, to predict environmental changes. We discuss traits adaptive to such unpredictably-changing tropical environments. Separation of predictability of temporal environmental change and synchronous changes among patches improves our understanding. Low oviposition rate and resulting prolonged life-span of *Epilachna vigintioctopunctata*, usually associated with *K*-selected traits of life history, seem to be adaptations for unpredictable environmental changes.

Keywords. Aseasonal tropics; unpredictable change; population dynamics; life-history strategy; stingless bee; lady beetle.

1. Introduction

Until recently, equatorial tropical environments had been thought to be constant. The absence of catastrophic reductions in population density due to seasonal fluctuations of physical environments is one of the basic conditions for *K*-selection (MacArthur and Wilson 1967). However, in this decade, global climatic changes have been found to have catastrophic effects even in tropical environments (Glynn 1990; Ashton 1993; Lugo and Waide 1993). Although air temperature is highly constant in tropical environments, temporal fluctuation of rainfall is no more stable than temperate zone environments (Wolda 1978a, b). If tropical environments are not stable but rare disturbances occur at longer intervals, we need long-term studies of population dynamics that cover whole episodes of environmental changes in order to understand their impact. Only such long-term studies can detect influences of rare disturbances on animal populations and adaptive traits associated with them (Wiens 1977, 1984; Pickett and White 1985; Andrews 1991).

Studies on the phenology and population dynamics of tropical animals have recently increased, but information is still very limited, compared to such studies of temperate animals. This is especially true for the humid aseasonal tropics because previous studies have mainly been done in the seasonally dry tropics in Panama (Wolda 1978a, b, 1982, 1983, 1988; Leigh *et al* 1982; Wolda and Roubik 1986; Boreham and Roubik 1987; Roubik and Ackermann 1987; Roubik 1989; Andrews 1991) and Africa (Gibbs and Leston 1970; Owen and Chanter 1972; Young 1982). The central regions in the Southeast Asian tropics, Sumatra, the Malay Peninsula and Borneo are unique due to their lack of a distinct dry season, as shown by long-term average monthly rainfall, > 200 mm (Inoue and Nakamura 1990; Appanah 1993).

Another bias of previous studies in the tropics is that most population dynamics were described by indirect methods, *e.g.* light trap and chemical bait (*op. cit.*). These methods are suitable to obtain quantitative data at the community level but they do not reveal mechanisms that determine population change. Analyses of birth and death processes of individual life-histories are indispensable for such purposes, and may also provide insight on selection pressures concerning particular traits.

In Sumatra, Indonesia, we studied population dynamics of two groups of insects that have extremely different life-history traits by directly monitoring individual birth and death processes. The ladybird beetles considered here are solitary phytophagous insects of which we studied 24 generations during 37 months. Stingless bees are highly social insects that use flowers as food resources. Their life takes place mainly within the nest, which provides shelter from external hazards and also storage space for food. We studied 3·7 generations during 56 months. We hope to show how their comparison provides a deeper understanding of several different ways for animals to adapt to unpredictably-changing environments. Finally, our census period totally covered the El Nino-Southern Oscillation (ENSO) in 1982-1983 that was thought to be the strongest in this century (Philander 1989; Glynn 1990). Thus, our study can show responses of animal populations to this relatively rare event.

2. Unpredictable change in tropical climates

Regions of the tropical rainforest zone in Southeast Asia have been thought to be

under stable weather conditions, based on the long-term average of climatic data. There are no distinct dry seasons, defined as months with less rainfall than expected transpiration, that is with rainfall of ≤ 100 mm in the tropics (Myers 1980). This is highly favourable for activity and reproduction of many animals and plants (Whitmore 1984). At our study site, Padang, Sumatra, for example, average monthly rainfall exceeds 200 mm and this amount is, if sustained in individual months and years, enough to maintain soil humidity and plant growth without interruption (Inoue and Nakamura 1990). However, in this decade, "abnormal" deviations of climate have been reported from various regions from the world.

Recent attention to abnormality of global environments is partly due to development of methods for analyzing time series data and partly due to directional environmental changes that are caused by human activities, e.g. the concentration of CO₂ and other greenhouse gases. Especially, the ENSO has been found to have a strong influence on biotic communities on both sides of the Pacific Ocean (Glynn 1988, 1990, 1991a, b). ENSO refers to the interacting global atmospheric and oceanographic conditions that sporadically alter large-scale rainfall, ocean currents, etc., largely in the tropical and subtropical latitudes of the Pacific Ocean (Glynn 1988; Philander 1989).

In Asia, ENSO brings drier seasons. In the 1982–1983 ENSO, in east Indonesian islands there was virtually no rain for over 8 months and the total amount of rainfall dropped to 10% of the long-term average (Flohn 1986). Vast forests were devastated by fire in east Kalimantan (Malingreau 1984; Leighton and Wirawan 1986). Such catastrophic events must have a great influence on the population structure of rainforest plants, and animals that directly or indirectly depend on them. However, little information exists on responses of plants and animals to such catastrophes (Ashton 1993). Effects of ENSO in eastern coasts of the Pacific Ocean are reported from corals (Glynn 1988, 1990, 1991a, b) and from forests (Leigh *et al* 1990; Wright and Cornejo 1990; Wright 1991). The average interval of ENSO is 4 to 5 years but its periodicity and intensity greatly change from time to time, as shown below.

The influence of ENSO decreases in western regions of Asia where the monsoon becomes a more prominent cause of environmental change. During the 1982–1983 ENSO, the decrease in rainfall was 50% in Sumatra. In India the rainfall decrease was less compared with other average dry years (see figure 1, Mooley and Shukla 1987). The periodicity of the monsoon is two years; a strong monsoon follows a weak monsoon alternately (Yasunari and Seki 1992). The Asian monsoon essentially comes from the heat exchange system between the Indian Ocean and the Tibetan highlands; rainfall intensity during the monsoon season is negatively correlated with the amount of snowfall in Tibet during the previous winter. The possible lag effects of snow cover on the monsoon cycle have not yet been clarified (Yasunari and Seki 1992).

Figure 1 illustrates another characteristic of rainfall patterns. Although ENSO and the monsoon are important factors, their intensities and intervals change greatly in actual time series. Spectral analysis based on the maximum entropy method can detect the relative importance of different periodicities of fluctuation. We applied this method to rainfall data in west Indonesia (figure 2, Yasunari and Suppiah 1988; Inoue and Nakamura 1990). In this region, the major peak is found at around 4 to 5 years, corresponding to the periodicity of ENSO. But this peak is not sharp; which implies that the periodicity of ENSO is not fixed and may change

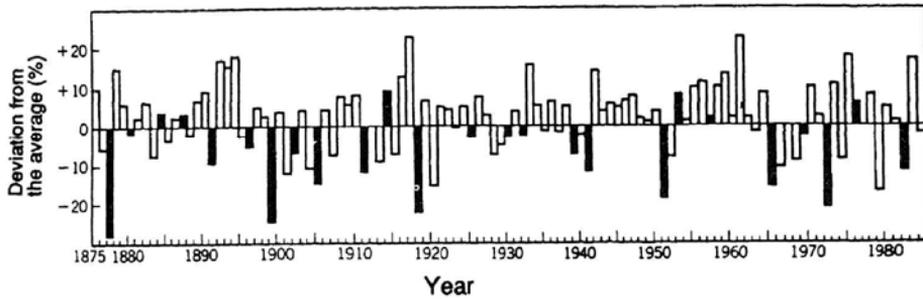


Figure 1. Change of rainfall during the monsoon period in India. Filled bars shows El Niño and Southern Oscillation (ENSO). Redrawn from Mooley and Shukla (1987).

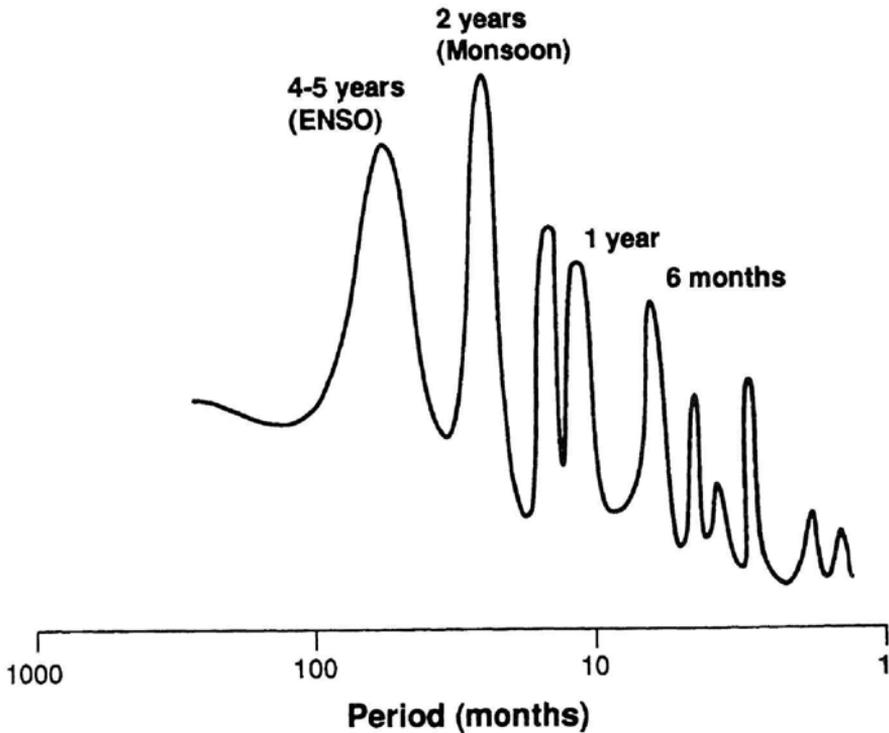


Figure 2. Power spectrum of rainfall that shows predominant periodicities, 4-5 years (ENSO), 2 years (monsoon), 1 year, 6 months and others, in Java and Sumatra. Redrawn based on figures 5 and 7 of Inoue and Nakamura (1990).

greatly. The 1982–1983 ENSO drought event in east Asia was a remarkably strong event, probably the strongest of this century. An ENSO of this magnitude may occur at > 100 year intervals (Glynn 1988). The two-year period of the monsoon is sharper and has the second highest spectral power function, shown by the area under the spectrum curve. Periodicities that originated from annual movement of

the sun (6 and 12 months) are distinct but their power function is weak and, moreover, there are several periodicities in the range from 25 days to 2 years. This implies that a change of daylength cannot be used by animals and plants as an indicator of seasonal change, as it is in the temperate region (Tauber *et al* 1986; Masaki 1990).

To summarize, environmental conditions in the Asian tropical rainforest region are favourable for plants and animals throughout an average year. Nonetheless, occasional droughts occur at various periodicities and various intensities. The predictability of environmental change is apparently quite low in this region. Then how do animals regulate their life cycle (if at all) in such unpredictably-changing environments? To answer this question we studied population dynamics of insects from 1981 to 1985 which covered the 1982-1983 ENSO. Our study site, Padang, Sumatra, nearly lies on the Equator (0.53° S, 100.21° E), and is predominantly with a tropical humid equatorial climate: Mean monthly air temperature fluctuated only between 26.7° C and 27.5° C and the annual rainfall was 4100 to 4800 mm without a clear alternation of wet and dry seasons. However, rainfall changed greatly from month to month during our census period, 1981 to 1985 (figure 3). General climatic conditions of Sumatra are given in Inoue and Nakamura (1990).

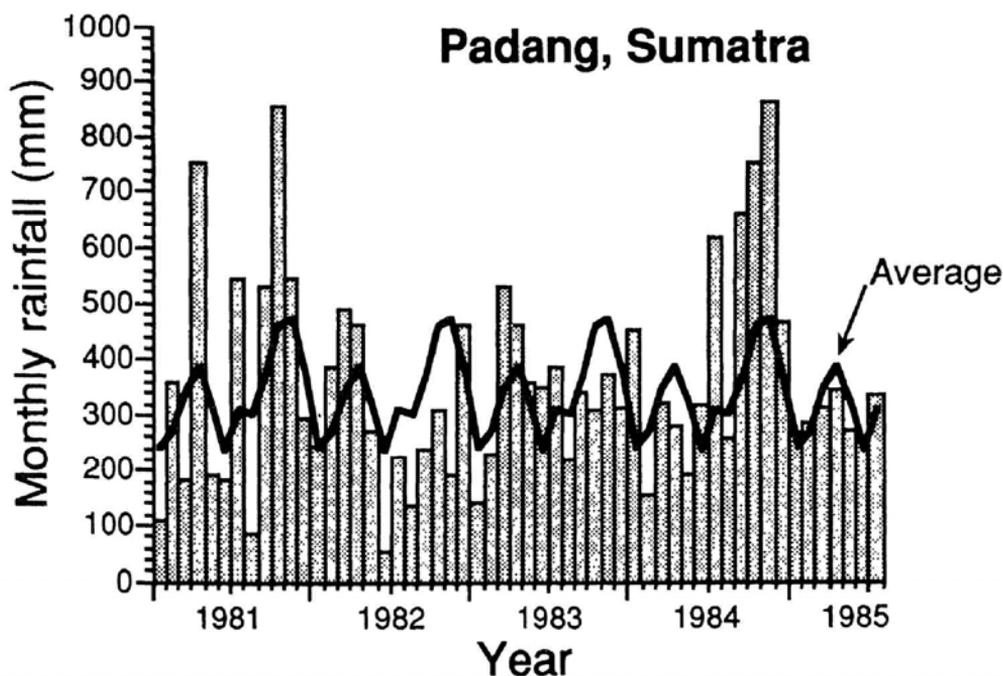


Figure 3. Monthly rainfall during the census period from 1981 to 1985 in Padang, Sumatera Barat, Indonesia, with the long-term average pattern.

3. Population dynamics of solitary beetles

3.1 Beetles

The 28-spotted lady beetle, *Epilachna vigintioctopunctata* (Fabricius) (henceforth abbreviated as *Evp*) feeds on a perennial shrubby weed, *Solanum torvum*

(Solanaceae). *Epilachna* beetles also become serious pests of solanaceous crops such as eggplants and potatoes over a broad geographical area from Japan (Nakamura 1976a, b, 1983; Hirano 1985a, b) to South Asia and Australia (Kalshoven 1981; Richards 1983). *Evp* is one of the most abundant epilachnine beetles in the Province of Sumatera Barat (Katakura *et al* 1988) and we have studied geographical distribution and host plants of the genus *Epilachna* (Abbas *et al* 1988; Katakura *et al* 1988), survivorship and fertility schedules under laboratory conditions (Nakamura *et al* 1984; Abbas *et al* 1985), and field population dynamics (Abbas and Nakamura 1985; Nakamura *et al* 1988, 1990).

3.2 Study site and methods

The study was carried out from January, 1982 to January, 1985 in a farmer's garden at Ulu Gadut in the southwestern environs of Padang (140 m alt.). There were 30 plants of *S. torvum* in the study site of 0.24 ha and they were isolated more than one kilometer from other host plant patches.

Censuses were carried out at 3 to 7 day intervals. The adult population was censused by mark and recapture methods and population parameters were estimated by the Jolly (1965)-Seber (1973) method. The adult's residence time in the study site (patch) was estimated by the difference between the date of first finding and the date of the last recording (sighting) of individual beetles. This parameter is affected by adult longevity because our census method could not distinguish emigration from death. Immatures (egg to pupa) were counted directly. Host plant conditions, e.g. the number of leaves, fruits and flowers, and the intensity of feeding were censused monthly. Detailed procedures are described in Nakamura *et al* (1988, 1990).

3.3 Results

Adult abundance fluctuated at a magnitude of 300 and exhibited three major peaks during the three years (figure 4). Population increase started at the 1982-1983 ENSO and then took three generations to reach a peak. Population decrease was gradual and, as shown later, the main cause was decrease of host plant abundance. The adult population did not increase in 1984 and this was related to heavy rainfall from September to December.

Compared to the rather gradual changes in adult population, oviposition intensity increased at an interval of about 48 days, showing discrete peaks. Peaks were especially clear during phases of population increase. This discreteness continued during the following immature stages and, as a result, adult emergence was also discrete. We have not yet explained why generations were discrete. This is an interesting phenomenon because the theory of population ecology based on the Leslie matrix tells us that, under stable conditions, proportions of developmental stages soon reach a stable, overlapping distribution. Parasitism was not responsible for this discreteness of population fluctuation because the per cent parasitism in both egg and pupal stages was rather constant over discrete fluctuations of beetle density (figure 3 in Nakamura *et al* 1990). Godfrey and Hassell (1987, 1989) proposed a model to explain discreteness of generations in constant, "tropical"

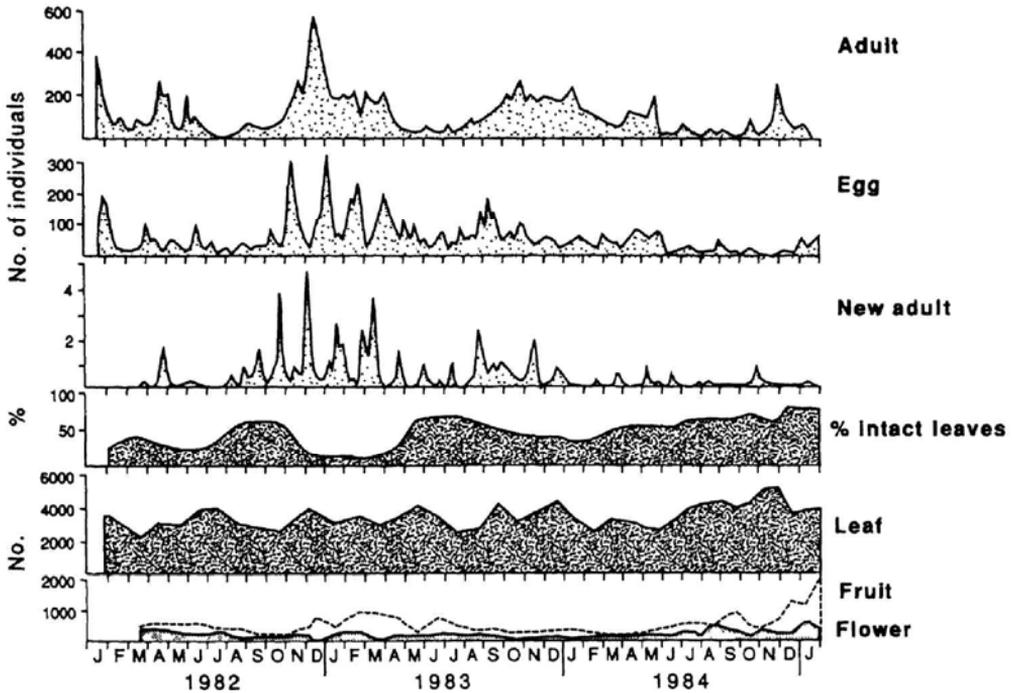


Figure 4. Fluctuation of the number of the lady beetle, *Evp* and phenology of its host plant, *S. torvum*. From top to bottom, the total number of adults, the number of eggs, the number of newly emerged adults, and the percentage of intact leaves, the total number of leaves, the numbers of flowers and fruits, respectively.

environments, based on the host-parasitoid interaction. But their model cannot be supported in this study because parasitism did not increase prior to decrease of beetle density.

The total number of leaves in the study site did not change greatly, but the percentage of intact leaves decreased notably during phases of population decrease (figure 4). Thus, food abundance was one factor that suppressed population density but this operated only at decreasing phases after high density, as shown below. Flowering and fruiting continued aseasonally throughout the year.

When host plants were intact, average adult residence time in the study site decreased significantly (F -test, $P \leq 0.01$) with an increase of monthly rainfall (figure 5). When host plants were severely defoliated, the average time of residence did not change in response to rainfall but it was significantly lower than that at periods when host plants were intact (Mann-Whitney test, $P \leq 0.002$ when monthly rainfall ≤ 400 mm). Rainfall also significantly ($P \leq 0.002$) lowered hatchability of eggs when host plants were intact (figure 6). However, hatchability did not significantly depend on host plant condition (figure 6).

Rainfall affected population fluctuation through two routes as shown above. Rainfall lowered egg hatchability and time of an adult's residence in the study site. But rainfall (x) did not influence the intensity of parasitism on eggs ($y\% = 0.29x + 13.9$, $r^2 = 0.032$) or the survival rates of larvae ($y\% = 0.11x + 79.7$, $r^2 = 0.001$) and pupae ($y\% = -0.77x + 19.4$, $r^2 = 0.15$). The number of eggs produced

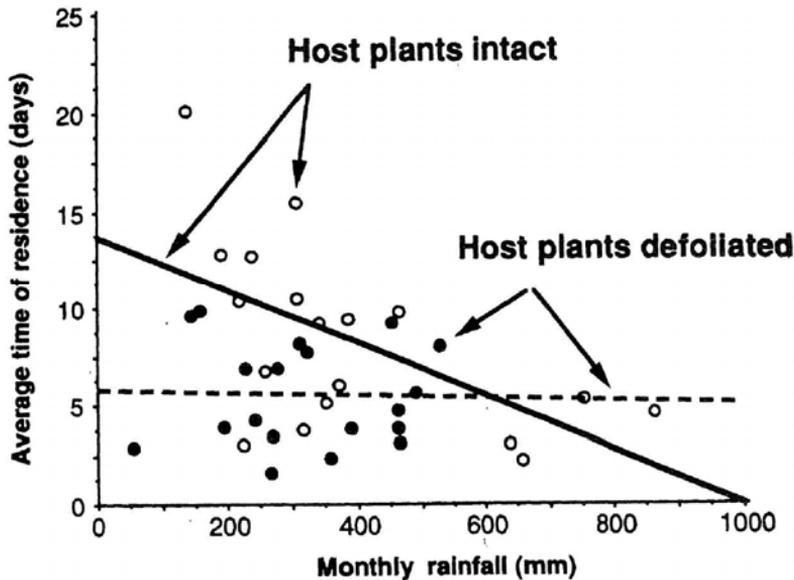


Figure 5. Average time y that individual beetles stay in the study site (patch) as a function of monthly rainfall x . When host plants were intact (during phases of population increase, Jul.-Dec, 1982, Jun.-Nov., 1983 and Jun.-Nov., 1984, and the percentage of intact leaves was $> ca$ 50%), $y = 0.014x + 13.7$ ($n=18$, $r^2 = 0.34$, $P = 0.01$), and, when host plants were severely defoliated (during phases of population decrease, Jan.-Jun., 1982, Jan.-May, 1983, Dec, 1983-May, 1984 and Dec, 1984-Jan., 1985, and the percentage of intact leaves was $< ca$ 50%), $y = 0.001x + 5.8$ ($n=19$, $r^2 = 0.001$, $p = 0.89$).

per female also decreased with an increase of rainfall. Because the total number of eggs produced per generation is the product of adult residence time and per-capita fecundity, it decreased with an increase of rainfall. Thus, our conclusions for the *Epilachna* beetle rest on two points. First, in months with rainfall of ≥ 300 mm, the normal conditions in our study area, population increase was suppressed by rainfall. Any decrease of rainfall due to ENSO or other causes releases this condition. Secondly, when rainfall is not limiting, population density then can be controlled mainly by food abundance. Such food shortage was rare and only occurred after the population increased for more than three generations.

4. Colony population dynamics of social bees

4.1 Stingless bees

We have found 24 stingless bee species (Meliponini, Apidae) and three honey bee species (Apini, Apidae) in Sumatera Barat (Sakagami *et al* 1990; Salmah *et al* 1990). The stingless bee, *Trigona (Tetragonula) minangkabau* Sakagami and Inoue, studied here, was most abundant in both lowland and highland primary forests and was also found in secondary forests and disturbed areas (Sakagami *et al* 1983; Sakagami and Inoue 1985; Inoue *et al* 1990a; Salmah *et al* 1990). The nest sites of stingless

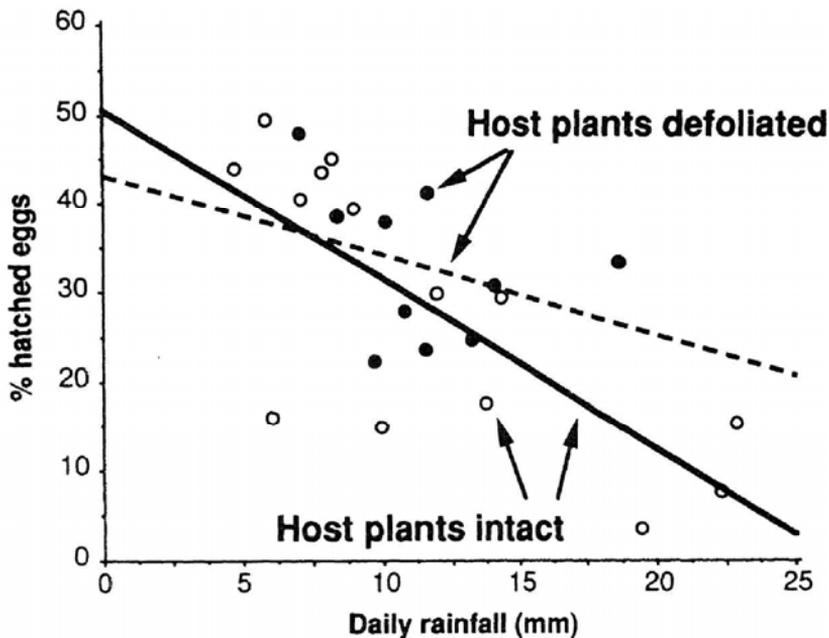


Figure 6. Percentage of hatched eggs (y) as a function of average daily rainfall (x) during the egg stage. When host plants were intact, $y = -1.9x + 50.5$ ($n=14$, $r^2 = 0.56$, $P = 0.002$), and, when host plants were severely defoliated, $y = -0.9x + 43.1$ ($n=10$, $r^2 = 0.117$, $P = 0.33$).

bees were essentially tree cavities and site preferences were size-specific; the largest were huge (>300 litre) nests of *T. canifrons* in emergent tree trunks in primary forests and the smallest (0.3 litre) nests of *T. fuscobalteata* in hollow tree branches (Salmah *et al* 1990). *T. minangkabau* built the second smallest (0.5 litre) nests in hollow tree branches of 20–30 cm in diameter (figure 7a). *T. minangkabau* also used man-made cavities, *e.g.* bamboo pillars (figure 7b) and spaces in house walls, as nest sites in disturbed areas (Sakagami *et al* 1983).

Mature colonies of *T. minangkabau* contained ca 3000 adult and ca 4000 immature workers, and the queen and several immature daughter queens (figure 7d, Sakagami *et al* 1983). About 80% of emerged daughter queens were killed by workers within a few days after emergence (Inoue *et al* 1984a, b). An exception was one daughter queen that emerged when her colony had just finished preparation of a new nest for colony foundation. The daughter queen emigrated to the new nest site with about 30% of the workers (Inoue *et al* 1984a). During favourable conditions, a colony could initiate foundation of a new nest each 6 months. Below we call colonies that reach this stage "mature" colonies, although colony development varies greatly from colony to colony. Another reason that newly emerged queens survived was the death of the mother queen. In this case, the daughter could supersede the queen.

4.2 Study site and methods

The study site, the Horticultural Experiment Station in Lubuk Mintrun, was at

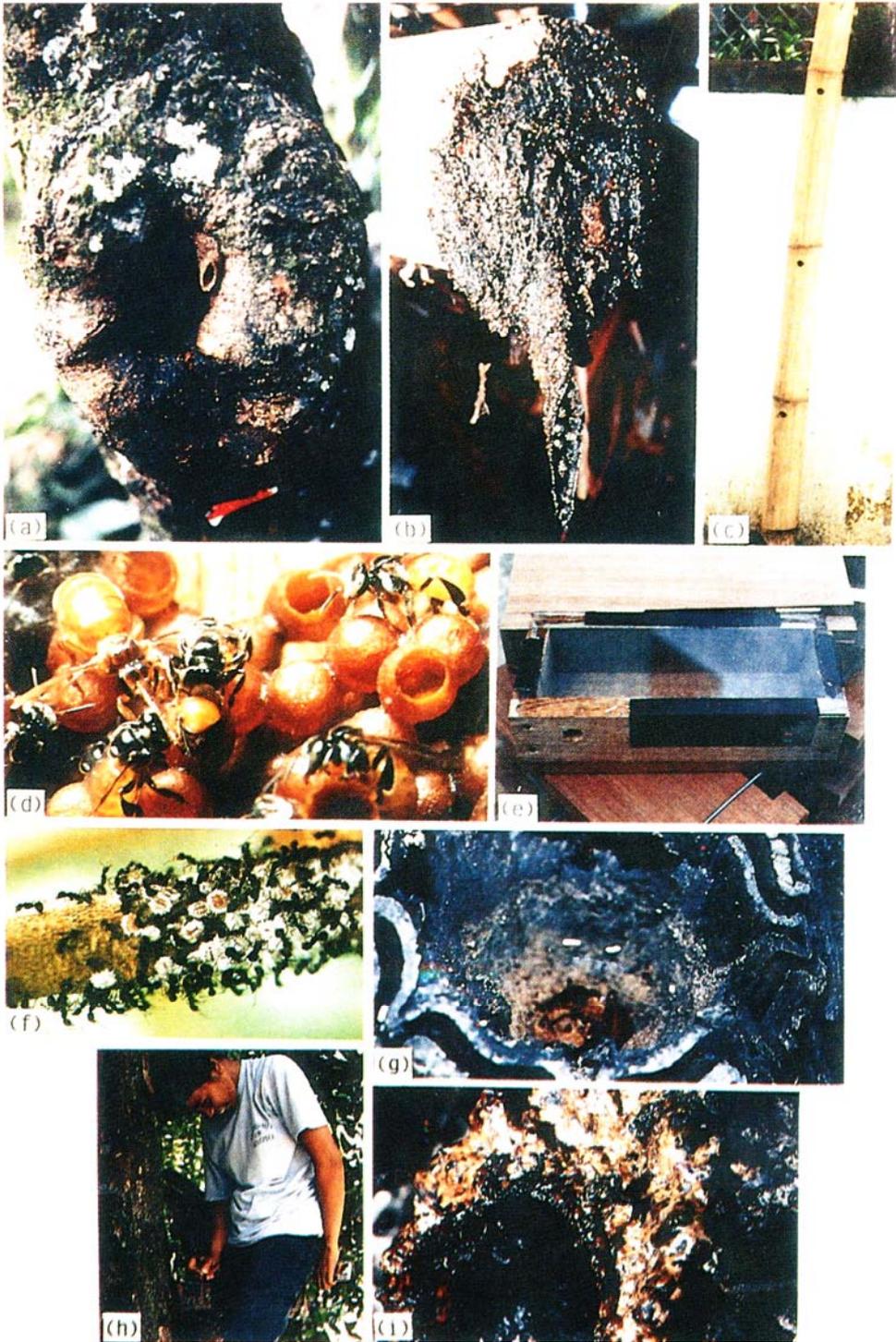


Figure 7.

20 m above sea level at the foot of the Barisan Mountains (figure 8). The main vegetation of the study site consisted of plantations of tropical fruits, e.g. rambutan, *N. lappaceum* (figure 8) and durian, *D. zibethinus* (ca 480 × 200 m, 8.6 ha). The first rambutans in the study site were planted in 1931 and had grown to a height of 10 m, their diameter was 50–60 cm at 50 cm above the ground.

We censused tree cavities and possible artificial nesting sites to estimate the number of natural colonies in the study site, in January, 1982, September, 1983, October, 1984 and March, 1987. At each census, two persons searched 4 days. We set 362 trap nests in the field, of which 248 were perforated bamboo stems (figure 7c, inner volume = ca 2 litre) and 114 were wood boxes with glass tops (figure 7e, inner dimension: 7 × 20 × 5(h) cm, 0.7 litre). Trap nests were set out in January, 1981 (100 traps), December, 1981–January, 1982 (138), December, 1982 (75) and October, 1983. Additions were made when trap nests were broken.

The census of occupation of trap nests continued weekly or bimonthly for 56 months from January, 1980 to August, 1985. In each census, we checked animals that occupied trap nests: *T. minangkabau*, 6 arboreal ant species [*Dolichoderus* sp., Dolichoderinae, coded as A1; *Camponotus* sp. Formicinae, A2; *Crematogaster* sp. Myrmicinae, A3; *Anoplolepis longipes* (Jerdon), Formicinae, A4; *Monomorium floricola* (Jerdon), Myrmicinae, A5; and *Polygraphists rastellata* (Latreille), ignored because of its low density], gecko lizards, etc. When wood boxes were used by *T. minangkabau*, we opened the top lid and made a map (figure 7h) of brood areas and storage pots through the top glass to estimate the number of workers and the amount of stored resources. Presence or absence of the queen was also checked (figure 7d, T Inoue, S Salman and Nismah, in preparation).

In addition to the above census of nest site occupation, nests at various times after foundation were collected at about one-year intervals, especially in August to September, 1983, for exact population count and resource measurement. The total number of collected nests was 28. Diurnal foraging activity was also observed weekly from January, 1981 to August, 1983 (T Inoue, S Salmah and Nismah, in preparation).

4.3 Results

In the study site we found 35, 39, 19 and 20 natural colonies, respectively in 1982, 1983, 1984 and 1987; 40% of natural colonies were found in tree hollows of rambutan (figure 7a), durian, or beringin (*Ficus* sp.), 40% were in hollow wooden ferns that were used to support orchids (figure 7g) and 20% were in spaces of house walls.

Trap nests were used by various animals (figure 9). Among these, 6 arboreal ant species were a competitor for the stingless bee, *T. minangkabau*. *Dolichoderus* A1 was predominant, occupying 93% of the total ant occupation counts, others were less abundant (*Camponotus* A2 2.7%, *Crematogaster* A3 1.3%, *A. longipes* A4 1.5%,

Figure 7. (a) A natural nest of *T. minangkabau* in a tree hollow of rambutan (*N. lappaceum*), (b) a nest of *T. minangkabau* in an artificial nest site, the bamboo pillar of a hut, (c) a bamboo trap nest, (d) the queen and workers at oviposition on a brood cell area, (e) wooden trap nests, (f) ants, *Dolichoderus* sp, guard an aggregation of scales, (g) water on the top of a nest of *T. minangkabau* in a vertical tree fern, showing guard bees on the entrance, (h) observation of inner condition of a nest and making a nest map, and, (i) ants tangled by sticky resin at a nest entrance of *T. laeviceps*.

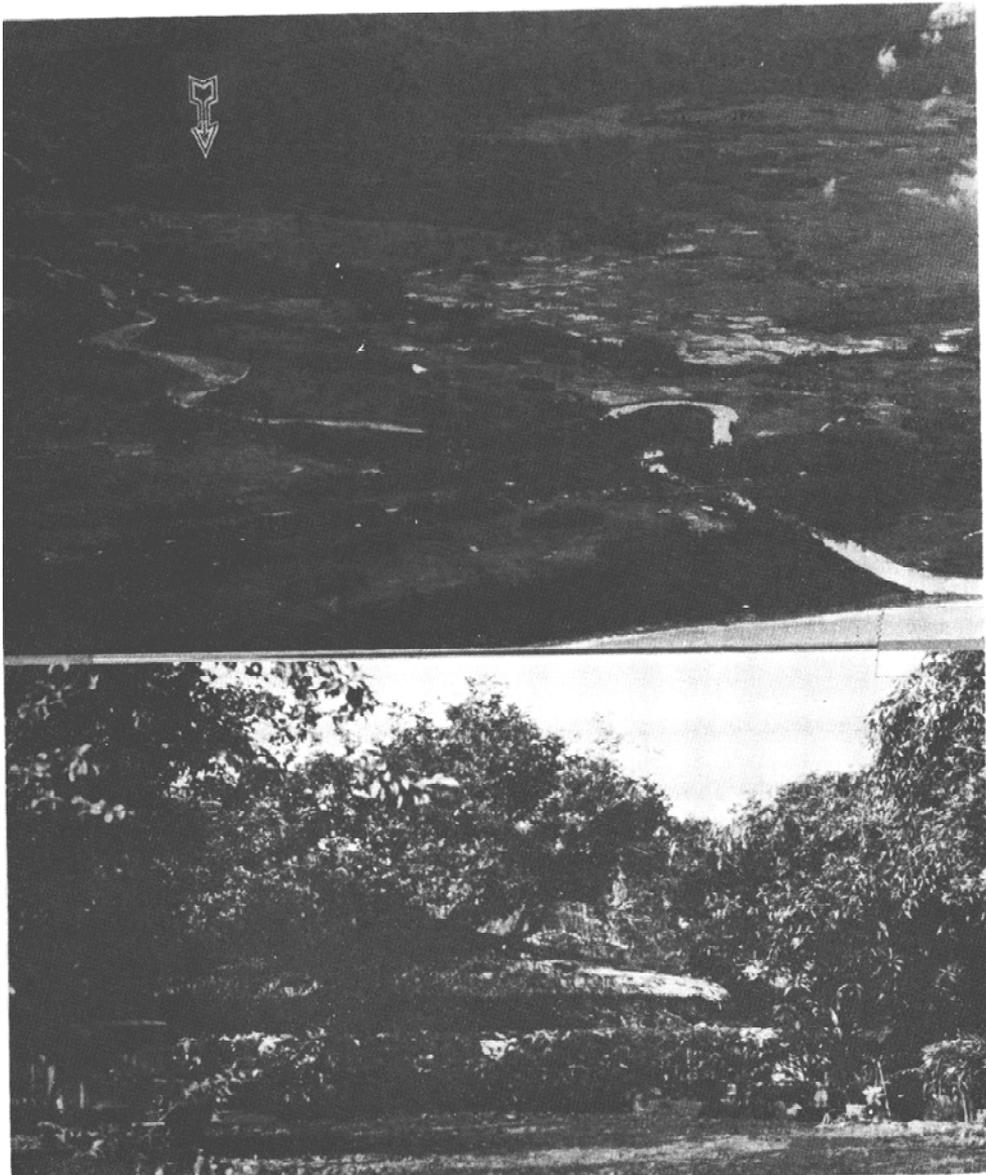


Figure 8. Habitat of the study site in Lubuk Mintrun, Padang, Sumatera Barat. (Top) the location at the foot of the Barisan Mountains; (bottom) the habitat: sixty year old rambutan trees.

M. floricola A5 0.5% and others 1%). These arboreal ants were nomadic and easily changed their nests by carrying immatures. But ants' distribution was limited to trees that were infested by scales (figure 7f) or aphids, which provided energy sources to ants. Ants guarded aggregations of these homopteran insects. As a result, trap nests that satisfied this condition were occupied by ants within three months after placement in the field.

Nests of three stingless bee species other than *T. minangkabau* were found in the

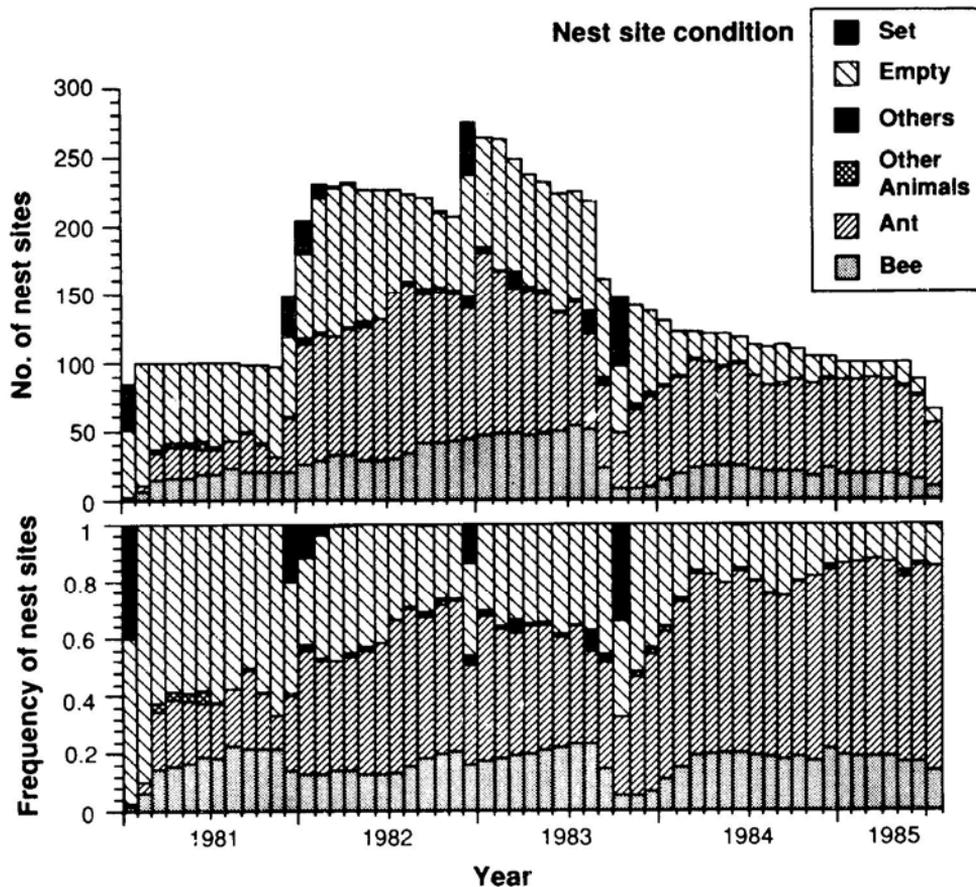


Figure 9. Changes in the number and per cent of nest sites occupied by several animals. Bee: occupied by the stingless bee, *T. minangkabau*; Ant: occupied by ants; Other animals: occupied by other animals, e.g., lizards; Empty: empty nest sites; Set: trap nests that are within a week after setting.

study site but only *T. minangkabau* nested in the trap nests. *T. itama* occasionally started deposition of resin around the entrance hole of trap nests, which indicated scouting at potential new nest sites, but all later abandoned. *T. itama* preferred larger cavities (ca. 3 litres, Salmah *et al* 1990). Size-specific preference for nest sites reduced overlap of nest site use. Occupation by *T. minangkabau* gradually increased after setting of trap nests (figure 9, Inoue *et al* 1990a; Salmah *et al* 1990).

After occupation by *T. minangkabau*, ants and other animals, empty trap nests decreased gradually to about 20% in 1984-1985 (figure 9). These empty nest sites were located at trees without scales and aphids or were located under dense tree foliage so that stingless bees never used them as nest sites. When we ignore these trap nests, almost all were used by some animals.

The number of *T. minangkabau* colonies steadily increased after trap nests were added (figure 10). In August and September, 1983 we collected 80% of *T. minangkabau* nests. The rate of increase of colony number was similar to that in the

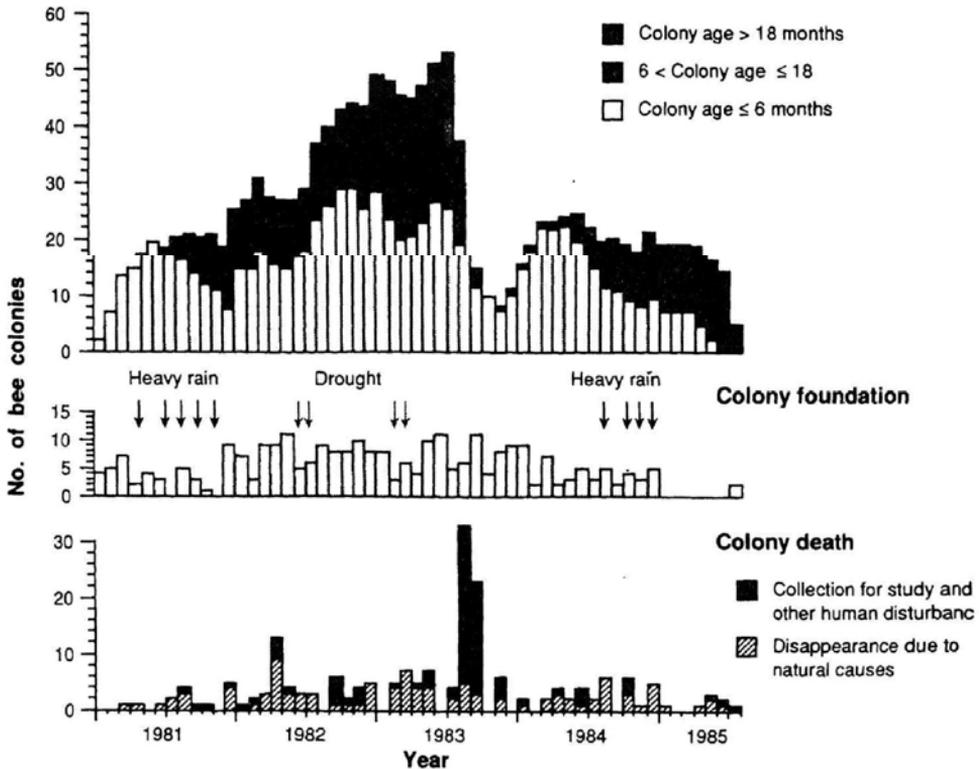


Figure 10. (Top) the number of stingless bee colonies that continued for ≤ 6 , ≤ 18 and >18 months after colony foundation. (Middle) the number of colonies newly founded. (Bottom) the number of colonies that disappeared due to natural causes and due to collection for study and other human disturbance.

first setting in 1981. Colony foundation continued at a rather constant rate throughout the year and there was no clear reproductive season. However, colony foundation significantly ($P \leq 0.003$) decreased during drier months in the 1982-1983 ENSO and during months with heavy rain before and after the ENSO (figure 11). Colony disappearance due to natural causes did not show any seasonality (figure 10). As a result, colony age distribution had gradually approached stability in the middle 1983 just before experimental collection by us.

T. minangkabau preferred empty trap nests to ones occupied by ants and conspecific bees. Relative preference for trap nests occupied by ants was estimated to be about 20% of that of empty ones, and that for trap nests occupied by bees was 6% (table 1). The cost of takeover of occupied trap nests may be the reason of lower preference for them.

The number of colonies founded per month (z) was basically determined by the number of matured colonies (y) in the study site and the deviation of rainfall from the long-term average ($|x-m|$, $m =$ the average, 350 mm), $z = 6.6 + 0.087y - 0.012|x-m|$ ($r = 0.55$, $P \leq 0.01$). This implies that the probability that a mature colony founds a new colony was 0.087 per month. The number of natural colonies that nested in natural tree cavities was estimated, by the above equation, to be 76 ($= 6.6/0.087$) in

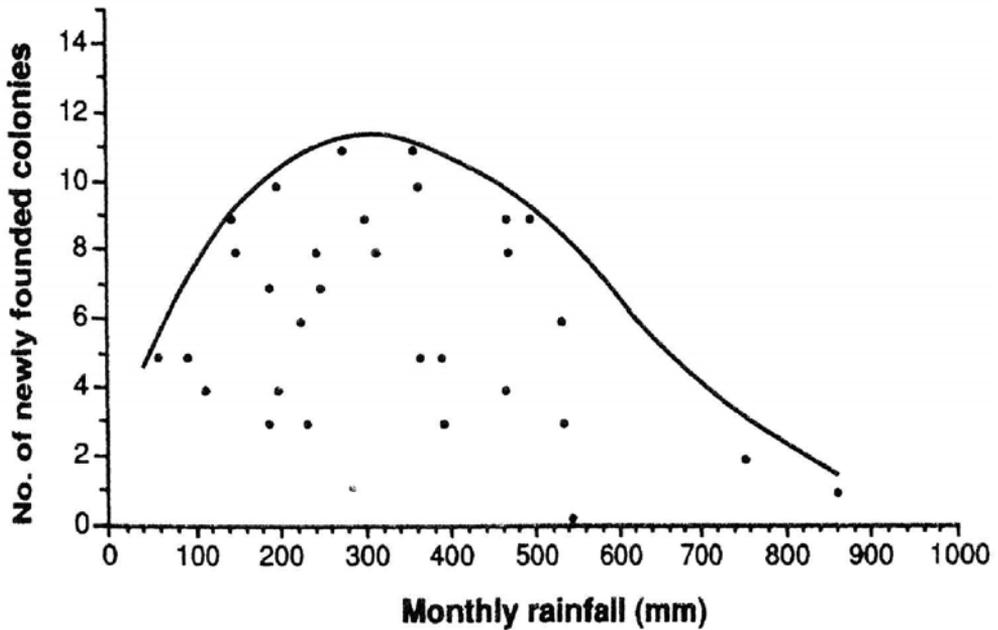


Figure 11. The number (y) of newly founded colonies per month as a function of monthly rainfall (x). y decreased significantly as a function of the deviation of rain fall from the average ($m = 350$ mm), $y = 8.1 - 0.014 |x - m|$ ($P \leq 0.003$).

Table 1. Relative preference of the stingless bee, *T. minangkabau*, for trap nests occupied by ants and conspecific bees, estimated by dividing the number of scoutings to each type by the average number of trap nests of each type.

Types	No. of scouts	Ratio	Average no. of trap nests	Ratio	Relative preference
Empty	206	1	54.4	1	1
Ant	61	0.3	68.1	1.25	0.2
Bee	6	0.03	25.8	0.47	0.06

or around the study site. As already shown, we found 20 to 40 natural colonies in the study site. The difference between the two values is the contribution of natural colonies around the study area.

Table 2 shows the life table of *T. minangkabau* colonies. There were 65 scouting episodes that stopped before mass migration of the new queen and workers. This means that at the scouting stage bees assess suitability and/or availability of nest sites. This category does not imply a true initiation of a colony and therefore is excluded from the analyses below.

Attacks by a conspecific colony occurred 4 times when a colony was about to establish a new nest (table 2). The attackers were bees from the nest neighboring the new nest site, usually within a few meters.

For highly eusocial insects, death of the queen usually implies the death of the whole colony, because the remaining workers cannot produce females. Colony disappearance due to queen death occurred mainly from several months to one year

Table 2. Life table of *T. minangkabau* colonies.

Months	Causes of colony death										
	SC	AT	QD	PC	AN	BN	UN	CN	HD	CL	Total
≤2	65	3	1	2	0	1	28	2	7	10	119
≤6	0	1	6	4	0	4	24	0	17	7	63
≤16	0	0	5	6	1	1	11	6	30	10	69
>16	0	0	0	0	1	2	3	6	8	1	21
Total	65	4	12	12	2	8	66	14	62	28	273

Months, Months after the start of scouting; SC, stop at scouting stage; AT, attacked by conspecific bees; QD, queen disappearance (successful supersedures = 4); PC, attacked by the coleopteran parasite, *C. wallacei*; AN, disturbed by ants indirectly; BN, nest site broken naturally or filled with water; UN, unknown causes; CN, alive at the census end; HD, human disturbance for honey collection; CL, collection for study.

cases of queen deaths). Stingless bees usually produce new queens at rather regular intervals and seem to try to increase the likelihood that the colony has some immature queens throughout the colony cycle, even when not ready for colony foundation (Inoue *et al* 1984a). By this mechanism, colonies of stingless bees can potentially continue indefinitely.

Attacks by the coleopteran parasite, *Coryphaeus wallacei*, de Marseul, 1864, Histeroidea, mostly occurred against established colonies and although the parasite was much stronger than bees and there was no defensive behaviour against this parasite, attack frequency did not increase so greatly (table 2). Once invaded, larvae of the parasite devastated the whole nest. Mortality factors for this parasite were unknown.

Attack by ants was never confirmed. Sticky resin barricades at the tip of the entrance tube were effective against ants, easily tangled by resin (figure 7i). Two colonies disappeared due to ants, because nest trees were severely infested by scales and the entrance tube became the foraging route of ants. In these cases, bees permanently closed the nest entrances making foraging impossible for the bee colony.

Breakdown of nest substrates was the most crucial mortality factor especially for relatively long-lived colonies (table 2) and that occurred usually after heavy rainfall (T Inoue, personal observation). In humid tropical conditions, microbes and fungi are thought to be active throughout the year and tree hollows themselves, that provided nest sites for stingless bees, are made by their activity. Thus, the factor that provided nest sites for stingless bees also brings serious mortality in advance of micro-organism's activity.

Human disturbance occurred mainly for long-lasting colonies that stored much honey. This was the most significant mortality factor for stingless bees that lived in the disturbed areas. Collection of honey by humans was also severe for honey bees, especially *A. dorsata*, which nests in open space (Seeley 1985; Inoue 1988). We did not find other mammals which attack nests of *T. minangkabau*. In primary forests mammals may become predators instead of man.

Survival rates of colonies were low during the first 6 months after colony foundation and 40% of colonies disappeared within 6 months (figure 12). After this period, the survival rate increased and became constant for a long period. Nearly

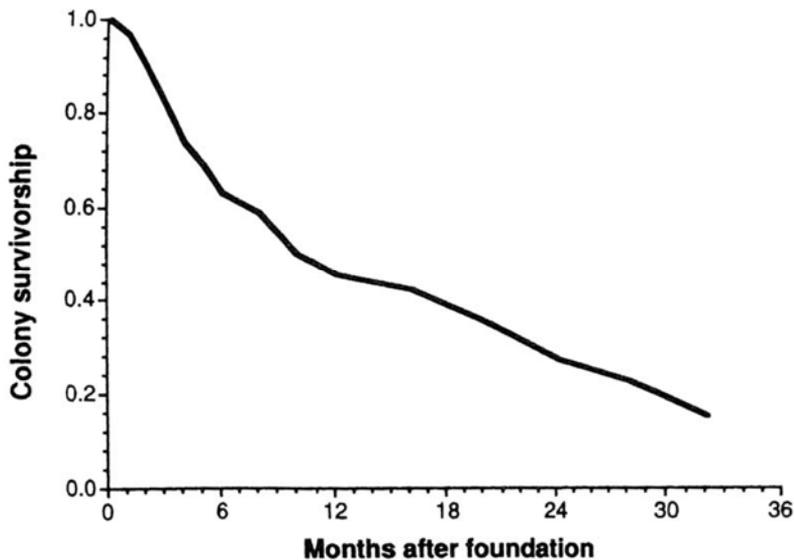


Figure 12. Colony survivorship curve as a function of months after colony foundation. Average duration of colony survival are 15 months for newly founded colonies and 26 months for colonies that survived the first 6 months after foundation, respectively.

20% of the colonies survived for 3 years. Expected colony persistence was 15 months for colonies just founded and 25 months for colonies that survived the first 6 months.

5. Discussion

5.1 Temporal patterns of environmental changes in the tropics

We have used "unpredictably-changing environments" without exact definition. Here we briefly review the idea of predictability of environments, based on Colwell (1974) and Stearns (1981). "Predict" means "say in advance that something will happen". In this sense, a constant environment is highly predictable because it is easy to say what will follow. The classical stereotypic image of the equatorial tropics falls in this category. Even if the climatic condition changes in time it is highly predictable if it repeats a single fixed pattern, such as a sine wave. The stereotypic image of temperate regions and seasonal humid tropics falls into this category. In such a simply cyclic environment, environmental cues that precede real change of season can be used for animals and plants to adjust their life cycle to the environment they live in, *e.g.* shortening daylength for overwintering (Tauber *et al* 1986).

Predictability is thus defined as the sum of constancy and contingency, and it becomes unity at the highest value (figure 13). As shown already, tropical rainforests are not under constant conditions and rainfall fluctuates greatly from month to month. Several predominant periods have been found in rainfall time-series in west

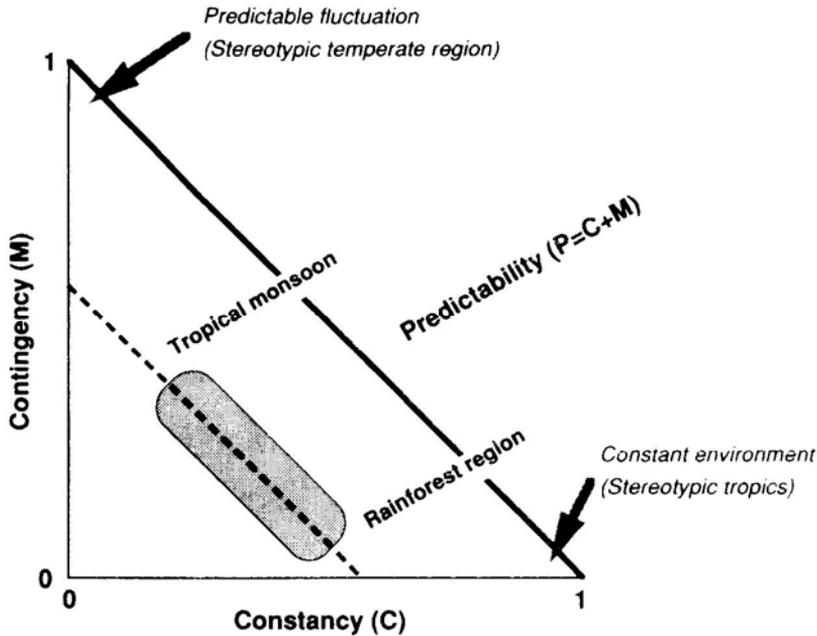


Figure 13. Schematic representation of predictability and its two components, constancy and contingency. Details are discussed in the text.

Indonesia (Inoue and Nakamura 1990), but this does not mean that temporal changes of rainfall there are simple convolutions of sine waves with different periods. Detected periods tell us only a portion of the real stochastic changes that occur in the global environment. In tropical monsoon and temperate regions, contingency may increase but still predictability would be lower than the previous expectation. In both temperate and tropical regions we have obtained little information about adaptive strategies of animals and plants in unpredictable environments, because, for this, we need long-term population monitoring of animals and plants that covers "unusual" events (Sousa 1984; Pickett and White 1985). Below we will review studies of phenology and population dynamics of tropical plants (§5.2) and animals (§5.3) and compare reproductive traits between tropical and temperate regions (§5.4), to reveal adaptive strategies in unpredictable environments.

5.2 Plant phenology in tropical environments

In the seasonal tropics in central America, there is a distinct alternation of dry (December-April) and rainy (May-November) seasons (Windsor 1990). Plant phenology is strongly influenced by the seasonal change of environments. Leaf fall is observed most frequently in the beginning of the dry season and flushing occurs in the beginning of the dry season in the wet Atlantic side and at the beginning of the rainy season in the dry Pacific side (Frankie *et al* 1974). Flowering of many trees occurs from the end of the dry season to the beginning of the rainy season (Frankie *et al* 1974; Haber and Frankie 1989), and fruiting continues in the rainy season

(Foster 1982). These seasonal patterns, however, do not cover all species in this region and there is wide diversity of phenology, *e.g.* extended flowering, among plant species, especially in shrubs, lianas and epiphytes (Bawa 1983).

Environmental cues for flowering have been studied by several authors in this region (Augsburger 1981, 1982; Wright and Cornejo 1990; Wright 1991). By watering the soil around roots of an understory shrub, *Hybanthus prunifolius*, Augspurger (1981, 1982) made plants flower outside the normal flowering season (usually a few days after the first rain). Thus, the proximate cue for flowering is soil humidity for this plant. She also found that an ultimate cause of synchronous flowering was pollination success and seed predation. Plants that flowered in the asynchronous period received lower service of pollinators, and resulting seeds were more highly attacked by predators than plants in the synchronous, normal period. Wright and Cornejo (1990) and Wright (1991) got different results by similar water-supplying experiments with different plants, *e.g.* *Piper*. They found flowering phenology was little affected, and endogenous rhythms were considered to be more important in determining the timing of flowering. Reich and Borchert (1984) clarified the importance of differences of water stress to plants at different topographical sites within a local community; even in dry forests, trees at wet sites experienced little or no apparent water stress. Hopkins and Graham (1989) cautioned that rainfall distribution is an inadequate measure of the seasonal availability of water for growth and reproduction of plants in Australian seasonal forests.

The impact of the 1982-1983 ENSO drought on a Panamanian semideciduous forest was examined by Leigh *et al* (1990). The drought in the 1982-1983 ENSO was the worst in two centuries at their site and tree mortality was 5 times higher than usual. The forest, however, recovered fully by the 1984 rainy season. They thought that the sharp dry season that came every year in this region seemed to have "preadapted" its forest for surviving the extraordinary drought without excessive damage. Animal populations were also little affected, as discussed below.

There are also seasonal regions in Southeast Asia, in Thailand and the Lesser Sunda islands (Inoue and Nakamura 1990) but there have been few and no quantitative phenological studies there. As already shown, in the central part of Southeast Asia rainfall continues throughout the year and there is no distinct dry season. Staggered (or mass) flowering of canopy trees, especially dipterocarps, is unique mainly to this region (see Appanah 1993). The interval of staggered flowering is irregular, between 2 to 10 years. Ashton *et al* (1988) found that the environmental cue for onset of flowering was a drop of $\geq 2^\circ$ C in daily minimum air temperature for ≥ 3 days. Such weather conditions most frequently appeared in ENSO. These supra-annual flowers are often pollinated by thrips which can increase their number quickly in response to the commencement of mass flowering. Yap and Chan (1990) found that essentially staggered-flowering species flowered even in years between mass-flowering years. In the sporadic-flowering years reproductive success of plants decreased due to higher seed predation, as found by Augspurger (1981). Ashton *et al* (1988) considered that seed predation was the ultimate cause of mass flowering of plants that belong to various families.

In addition to staggered flowering of above-canopy trees, Appanah (1981, 1990) classified three more types (synusiae) of pollination in the evergreen lowland forests of equatorial Asia: annual, rather regular flowering of above-canopy trees, extended or nearly continuous flowering of below-canopy plants, and synchronous, seasonal flowering of below-canopy plants. Most annually-flowering, canopy trees have large,

conspicuous flowers with ample floral rewards and are pollinated by large bees, birds and bats. On the other hand, staggered-flowering, canopy trees often have small flowers with reduced floral rewards and are pollinated by fecund, short life-cycle insects such as thrips. Below-canopy plants that flower nearly continuously have tiny flowers, pollinated by unspecialized insects. Seasonally-synchronous plants on the understory usually have powerfully smelling flowers that attract large traplining insects. Although we have not fully understood flowering and other phenological syndromes of plants in the aseasonal tropics, there are quite wide varieties of phenological patterns even in a local area and they are determined, at least in part, in relation with activity of animals, *e.g.* pollinators, seed dispersers, seed predators, and phytophagous animals.

5.3 *Animal phenology in tropical environments*

Seasonal abundance of animals varies considerably in both seasonal and aseasonal tropical environments. Wolda (1978a, b, 1982, 1988) reviewed seasonal patterns of insect abundance and found that clear seasonal peaks are more commonly observed in the tropics. Some insects only appear in a few months in each year and the life cycle is regulated by diapause, based on daylength and humidity (Tanaka *et al* 1987).

Wolda and Roubik (1986) monitored seasonal bee abundance by light traps in a seasonal forest in Panama. Most of 50 species were present throughout the year but some of them peaked during the dry-to-rainy transition or in the early rainy season. A stingless bee, *Partamona* aff. *cupira* was aseasonal but had abundance peaks during all but the mid-to-late rainy season. Time of peak abundance changed from year to year.

Seasonal abundance of euglossine orchid-bees was censused for 7 years at three locations in Panama and 51 species were studied by Roubik and Ackerman (1987). Most species were active throughout the year and many showed three annual abundance peaks. In contrast, only one genus, *Eufriesia* generally were present as adults only 1 to 2 months in a year. Euglossine bee populations were exceptionally stable, compared with other tropical insects and other temperate bees (Roubik 1989). The drought in the 1982-1983 ENSO gave little influence of seasonal abundance patterns according to both Wolda and Roubik (1986) and Roubik and Ackerman (1987), as reviewed by Leigh *et al* (1990). Further analyses by Roubik (personal communication, June, 1992) revealed that numbers of euglossines, honey bees and other bees increased > 50% in the ENSO years.

Swarms and nesting colonies of the Africanized honey bee were collected for four years from their arrival in Panama in 1982 (Boreham and Roubik 1987; Roubik 1989). Both swarms and nests were recorded throughout the year but peaked in the dry season and the early rainy season. The seasonal abundance pattern coincided with periods of floral abundance.

In the most of the above studies of insects, high stabilities of population changes were stressed, and even unusual strong drought in the 1982-1983 ENSO had little effects on them. In contrast, a study of a lizard in Panama (Andrews 1991) presented an example of an unstably fluctuating population. One population of the lizard locally became extinct for three years after the 1982-1983 ENSO. Widespread bleaching and mortality of reef-building corals occurred in the tropical eastern Pacific region during the 1982-1983 ENSO (Glynn 1990).

In our study site, the western slope facing the Indian Ocean in central Sumatra,

rainfall continues throughout the year and the annual total exceeds 4000 mm on the average and frequently is over 5000 mm. Such "usual" amounts of rainfall seem to be excessively humid for some insects as shown by our studies in epilachnine beetles and stingless bees. This was true even at community levels in some insect groups; the bee fauna was quite poor on the western slope and increased in richness in the drier eastern slope of the Barisan mountains (annual rainfall=2000 3000 mm, Inoue *et al* 1990a; Salmah *et al* 1990).

In the 1982 1983 ENSO, rainfall decreased moderately (50% of the long term average) in central Sumatra and this was favourable for epilachnine populations. Mechanisms of population increase were improvement of egg hatchability and time of adult's residence in a patch (or adult longevity) in the ENSO period. S Nakano, K Nakamura and I Abbas (in preparation) performed additional population censuses of the epilachnine beetle, *Evp*, by the same method of Nakamura *et al* (1990, this study) for 13 months from June, 1988. They simultaneously monitored 7 host plant patches, that were apart at least 1.5 km and at most 12 km from each other. In all sites, adult populations started to increase between December, 1988 to January, 1989. This implies that population increase was common to, at least, a local area of range of 12 km and might be influenced by common environmental factors. In December, 1988 and January, 1989, rainfall dropped to about 200 mm and this created favourable conditions for epilachnine beetles (see figures 5 and 6). Another interesting point S Nakano, K Nakamura and I Abbas found was that, after this increase of populations density, populations became extinct in two patches due to defoliation of the host plant. This implies that extinction at single patches may be rather frequent if we consider a time scale of over 10 years.

The dry ENSO period in 1982-1983 was slightly unfavourable for stingless bees, as the number of colony foundations decreased at both extremes, heavy rain and dry months (figure 11). But colony mortality was independent from the amount of rainfall. Nests of stingless bees are completely shielded by resin, except for a small entrance hole, and thereby free from the high humidity outside. Rainfall indirectly affected colony performance of stingless bees through restricting foraging duration. Thus, the duration of rainfall in daytime is a better indicator of the rainfall influence than the amount of rainfall. The stock of food resources gradually decreased when it rained for long time (T Inoue, S Salmah and Nismah, in preparation). Bees have the ability to predict the onset of rainfall, prior to an actual start, by change of light intensity (confirmed in greenhouse experiments, Tezuka, Y Maeta and T Inoue, unpublished results).

We confirmed that the limiting factor for colony density of the stingless bee, *T. minangkabau*, was nest site availability. The colony density was increased 2.5 times the colony density at natural cavities by experimental addition of artificial trap nests. Further increase of colony density of the stingless bee was suppressed by competition with arboreal ants for trap nests. Nearly 50% of added trap nests were occupied by ants. Floral resources were not a limiting factor because nests stored ample food resources even during rainy periods (T Inoue, S Salmah and Nismah, in preparation). This may have been due to our study site being located in an orchard area.

5.4 Comparison of reproductive traits between tropical and temperate regions

We find both behavioural and physiological divergence between tropical and

temperate groups of beetles. Ecological traits found in the tropics can now be appreciated as adaptive in unpredictably-changing environments, despite relative environmental stability.

The 28-spotted lady beetle, *Evp* is distributed also in temperate regions of east Asia where it feeds on potatoes and eggplants. We will compare reproductive traits of *Evp* between Sumatra (this study, Nakamura *et al* 1984; Abbas *et al* 1985, Abbas and Nakamura 1985; Nakamura *et al* 1988, 1990) and Japan (Nakamura 1976a, b, 1983; Hirano 1985a, b). In Japan *Evp* is mainly univoltine and partly bivoltine and below we neglect the second generation.

Reproductive rate per generation is more than four times higher in temperate Japan than in tropical Sumatra (table 3). Potential abilities of egg production, measured in laboratory conditions with excess food supply, do not differ between regions. Parasitism at immature stages is much higher in Sumatra than in Japan. This is a major cause of the low reproductive rate in Sumatra.

Table 3. Comparison of reproductive traits between tropical and temperate *Epilachna* beetles.

Traits	Tropical beetles	Temperate beetles*
Reproductive rate per generation	5.3	20–60
Immature period	23 days	26 days
Max. adult longevity	60 days	— — —
Max. no. of eggs per female	770	600–1000
Parasitism (%) Egg	25%	0%
Larva-Pupa	85%	1.6–3.8%
Food shortage	Rare	Frequent**
Time of staying in a patch	6–15 days***	17–20 days
Inter-patch movement	Frequent	Low, seasonal
Mortality during overwintering	—	96–98%

* Mainly based on Nakamura (unpublished results).

** Hirano (unpublished results) did not find food shortage.

*** 6 when host plants intensively fed on and 15 when host plant are intact in dry weather (this study).

We find two important differences in reproductive traits between the two regions. First, potential adult longevity measured in the laboratory is 60 days in Sumatra and this value is thought to be longer than that in Japan, although quantitative data are unavailable (table 3). As the potential number of eggs produced per female throughout the lifespan is similar, this means that the daily oviposition rate of the Sumatran beetles is lower than the Japanese epilachnine beetles. Sumatran beetles do not have a distinct oviposition peak soon after the onset of oviposition, while this is always the case in Japanese beetles. Thus, the Sumatran beetles employ a reproductive trait that is characterized by a slow oviposition schedule and they thereby enjoy a longer lifespan. A similar pattern has been found in other insects (*e.g.* a hemipteran bug, Carroll 1988). These characters (delayed senescence and slow reproduction) are confirmed to have a genetic basis (Rose and Charlesworth

1981; Luckinbill *et al* 1984 for *Drosophila*, Ohgushi 1991 for *Epilachna*). Trade-off between the two traits may exist in this *Epilachna* group but this topic is still controversial in general (Partridge 1989; Stearns 1989).

The second point concerns patterns of inter-patch movement of adults. The Sumatran beetles move actively throughout their lifespan. By dividing the potential adult longevity (60 days) by the average time of residence in a patch (6 days when host plants are severely defoliated and 15 days when host plants are intact during drier weather conditions), we can estimate that adults move over 4 to 10 patches during their lifespan in Sumatra. Higher activity of the Sumatran beetles has also been confirmed by direct observation of behaviour. The approach of observers evoked active flights on and around host plants (K Nakamura, personal observation). Such active flights are never observed in the Japanese beetles (K Nakamura, personal observation). On the other hand, inter-patch movement of the Japanese beetles depends on the phenology of host-plants. Once having arrived at a host plant patch from the hibernation site, overwintered adults do not emigrate from the patch even when host plants are severely defoliated (K Nakamura, unpublished results). Larvae produced later in the oviposition season frequently suffer from starvation because they cannot finish feeding before the end of the host plant season (Nakamura 1976a, b). Overwintered adults must compromise between decrease of offspring's survival rate due to defoliation and the probability that they cannot find another intact patch before the time when host plants will not persist as long as the immature period of offspring. Active inter-patch movements are observed in the first generation when their host plants, potatoes, are harvested. Adults of the first generation emigrate to find the second host plant, eggplant.

Higher reproductive rate of the temperate beetle is counterbalanced by heavy mortality during overwintering. Although adults enter a hibernation phase and overwinter in cracks in the ground, these adaptations are not complete and beetles suffer from low temperature during winter. On the other hand, mortality due to parasites is negligible in Japan. In Sumatra, even though parasitism is high on the average, it is not a key factor that regulates the population level (Nakamura *et al* 1990) because parasitism does not increase as a function of population density. Even in Sumatra the key factor is the availability of host plants.

For most weather conditions in Sumatra the population density of beetles fluctuates at lower levels and rarely reaches the level at which the density-dependent regulating factor operates. Heavy rainfall, the usual condition in our study site in Sumatra, suppresses population increase by lowering egg hatchability and decreasing the average time of an adult's residence. As the adult's residence time is affected by the adult longevity (see §3), a decrease of adult residence may reflect decrease of adult longevity from heavy rains. This restriction is lifted during the dry ENSO period. Moderate droughts (50% decrease) at ENSO periods are favourable for epilachnine beetles.

5.5 Social evolution in the tropics

For social insects, the nest is the information center and the colony as a whole can select only high-quality patches of flowers for foraging, avoiding low-quality ones (Seeley 1985; Roubik 1989). This means that the quality of a single patch does not directly influence the colony performance. Thus unpredictable changes within the

foraging range are stabilized at the colony level. As the foraging range of *T. minangkabau* covers an area within 500 m from the nest (Inoue *et al* 1985), the colony can thereby apparently stabilize spatial fluctuations in food supply within this area. Some other bigger stingless bees and honey bees cover an area within 5 km from the nest that would include various habitat types, some near rivers and under rather humid conditions even in dry seasons, and some on mountain ridges and under moderate humidity even in heavy rainy seasons.

The nest of social insects has another property. It functions as the ideal shelter against hazards outside the nest and against attacks by natural enemies. Even though heavy rain continues for several months, the inside of stingless bee nests is kept dry on account of the effective resin shield (figure 7g). And the nest provides storage space for food resources, from which bees can maintain their survival and reproduction even during flower dearth seasons (T Inoue, S Salmah and Nismah, unpublished results). Because of these two adaptive traits, colonies of social bees persist stably in environments that unpredictably fluctuate both in time and space.

Evolution of sociality in bees itself may relate to unpredictable change of environments. We have studied community structure of flower-visiting insects both in Sumatra (Salmah *et al* 1990; Inoue *et al* 1990a) and Kyoto (Inoue *et al* 1990b; Kakutani *et al* 1990; Kato *et al* 1990) by the same sampling method. The total number of bee species was 109 in Sumatra and 99 in Kyoto (figure 14). Thus, species richness of bees is not higher in the tropics than in the temperate region. This trend is supported by other studies of bees (reviewed in Roubik 1989; Inoue *et al* 1990a) and other examples in insects are shown in Price *et al* (1991). However, a clear difference is found in another aspect between the two regions; the percentage of social species was significantly higher in the tropics. All Apidae, which include stingless bees and honey bees, are social. Almost all Anthophoridae are solitary in the temperate region, but many social anthophorids are found in the tropics (Roubik 1989, 1990). In terms of individual abundance, nearly 80% of flower-visiting bees were social in Sumatra and about 40% in Kyoto (figure 14). Although we need further evidence, unpredictable environmental fluctuation may select for sociality, and the stabilizing ability of social bees has been demonstrated both in time and space. As individual workers in a single colony specialize on different plant species during foraging, the single colony of social bees becomes a pollination agent for multiple plant species.

In solitary insects, other traits are adaptive for unpredictable climatic fluctuations. As already shown, compared with the temperate species the tropical *Epilachna* beetle has a much longer life-span and much lower daily oviposition rate. These beetles move between host plants more frequently in the tropics, and take flight more readily. Although these traits are adaptive in the face of unpredictable climatic fluctuations, the time scale (2 months) that beetles can stabilize is far shorter than the predominant period (2 or 4-5 years) of climatic changes. This may be a cause of high population fluctuation and local extinction.

5.6 *Ecological traits in unpredictably-changing tropical environments*

The theory of *r*- and *K*-selection contrasts the two environmental conditions but this dichotomy appears not to explain ecological traits in the tropics. MacArthur and Wilson (1967) and Pianka (1974) did not distinguish constancy and

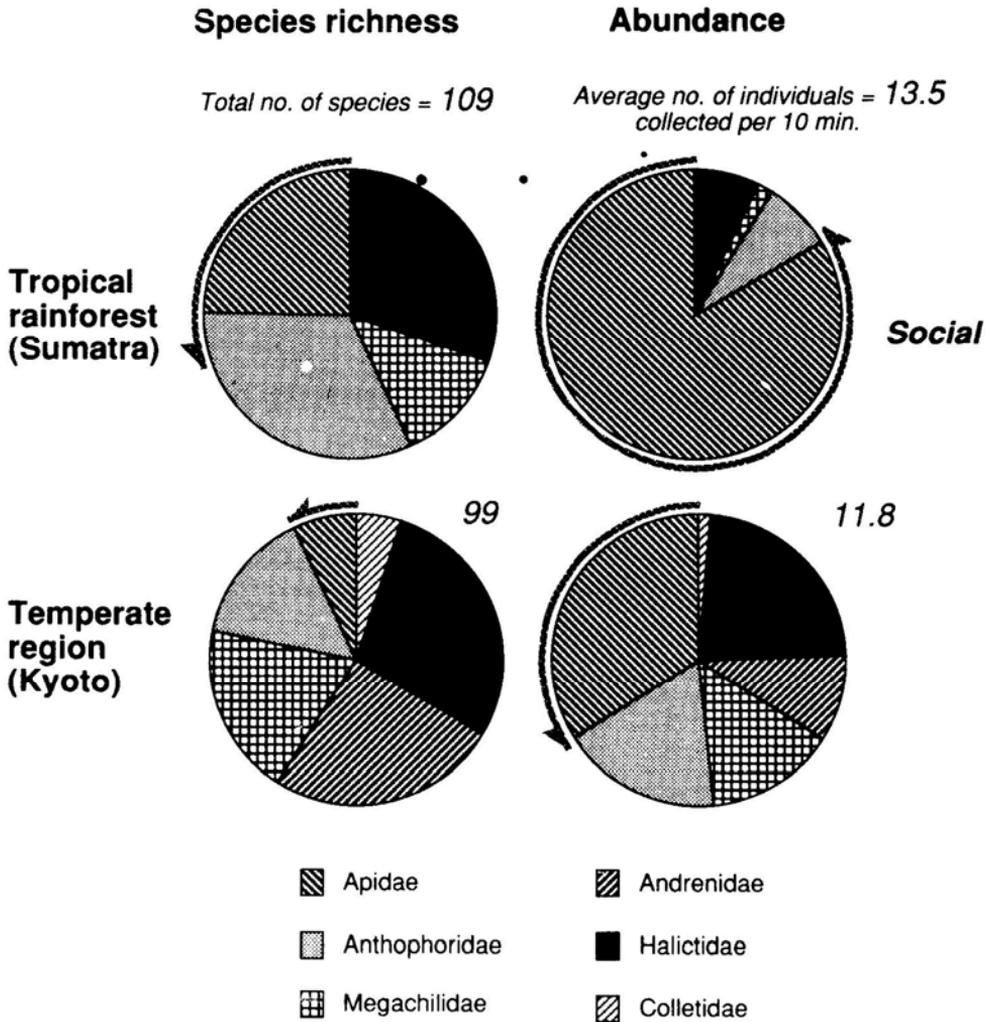


Figure 14. Comparison of species richness and individual abundance of bees between Sumatra and Kyoto, Japan. Original data are shown in Inoue *et al* (1990a) for Sumatra and Inoue *et al* (1990b), Kato *et al* (1990) and Kakutani *et al* (1990) for Kyoto. Social species are shown by arrows.

predictability, and thought that variable and/or unpredictable environments selected for *r*-strategists and constant and/or predictable environments selected for *K*-strategists. In completely constant environments in the laboratory, population density tracks the carrying capacity of experimental conditions. In such conditions, higher competitive ability must be selectively advantageous because this is the only selection pressure in such ideal conditions. The above authors considered that tropical environments were fairly constant and *K*-strategists were selected for. However, as shown in §5.1, tropical climates change greatly in an unpredictable manner.

Separation between predictability of the temporal environmental change in a

patch and synchronousness of temporal changes among patches improves our understanding of several ecological traits that were previously sorted into either *r*- or *K*-strategies.

First we consider cases at which synchronousness of temporal changes among patches is high. In these cases, emigration from a patch that is unfavourable for reproduction is not adaptive because other patches are also synchronously unfavourable. When predictability of the temporal change in a patch is high, onset of "resting for a fixed period" at the beginning of an unfavourable season may be the best strategy. Diapause of insects found in the seasonal tropics belongs to this category (Tanaka *et al* 1987). In the winter of southern Brazil stingless bees stop brood rearing and adult workers stay in the nest, reducing the amount of labour (S F Sakagami, personal communication). The number of workers decreases and the age structure becomes biased to older individuals. This is an example of resting in social insects.

When environmental predictability is low and changes among patches are synchronous, resting for a fixed period cannot be adopted by animals because the unfavourable condition changes unpredictably, not at a regular interval, to the favourable condition and *vice versa*. Enduring or resting at the level at which reproduction can be resumed quickly may be an alternate trait adaptive to such environments, because high air temperature in the tropics increases survival of animals, unlike the cold temperate winter. Our study area in Sumatra seems to conform to this category. There, stingless bees rear brood even in flower dearth seasons, and the complete cessation of brood rearing as in Brazil has been never observed. Hoarding of food during favourable foraging periods serves as an ecological adaptation for colony survival during unfavourable foraging periods. Sumatran stingless bees stored honey that supported the colony members for more than a half year. Observed unfavourable foraging periods were shorter than this duration.

Active movements found in epilachnine beetles superficially seem to be maladaptive to the synchronously changing environment because, due to synchronous temporal changes among patches, the likelihood of finding a favourable patch is virtually zero when the original patch is unfavourable. But, if population density increases during favourable periods to the level at which competition for food occurs, oviposition in a single patch increases competition among siblings. This becomes clear if we consider the extreme case, in which only one individual can grow up to adulthood from a single patch. Severe food depletion occurred at the end of one favourable period (5 months in the 1982-1983 ENSO) and population decreased to 1/300 of the peak density at this time (figure 4). Population extinction occurred in other patches (§5.4). In epilachnine beetles, an ecological crunch (see Wiens 1977 for definition) occurred at this phase of competition. Another ecological crunch appeared in the heavy rainfall period that followed the ENSO.

When synchronousness among patches is low, there are both favourable and unfavourable patches simultaneously. If environmental predictability is high, active search for favourable patches will be selected for. As a result, spatial distribution of animals becomes coarse grained (see Wiens 1976 for definition) and most individuals stay in favourable patches until population density becomes high. When both synchronousness of food availability among patches and environmental predictability are low, *r*-strategies, especially higher *r* and active dispersal not

depending on the present patch condition must be selected for. Individual distribution must be fine-grained (Wiens 1976) from low to high population density.

Some traits, e.g. longer length of life, larger body size and repeated reproduction, previously categorized into *K*-strategies by Pianka (1974), may be adaptations to unpredictable environmental changes, because these do not directly improve competitive ability for resources. Instead, these traits are adaptations to endure unfavourable conditions, if their duration changes unpredictably.

Typology or dichotomy, such as *r*- and *K*-selection often becomes tautology (Peters 1976, 1991; Wiens 1977). To further understand the ecological traits evolved in tropical environments, both quantitative measurements of temporal changes and spatial distribution of environmental conditions, and long-term monitoring of population dynamics of animals in various environments sufficient to cover the rare ecological 'crunch' are indispensable.

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