Community ecology of small mammals
in a tropical rain forest of Malaysia
with special reference to
habitat preference, frugivory and population dynamics

マレーシア熱帯雨林における小型哺乳類の群集生態
－ハビタット選好性，果実食性，および個体群動態－

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CONTENTS

Chapter I. Introduction

The matter and energy flows in a food web have been one of the major topics in community ecology for a long time, and many studies on this issue have been carried out in the field or using theoretical models (Pimm 1991). Recently, Reagan & Waide (1996) made a huge effort to draw interconnections among all the species in a tropical rain forest in Puerto Rico. As their effort was concentrated on the description of prey-predator relationships in the community, other kinds of interactions were not dealt with sufficiently.

The diagram of a food web is a powerful approach to describe the numerical aspect of the system. The diagram shows how the system is driven by energy through the prey-predator relationships, however, it does not provide us any ideas how the community is maintained by the interactions among organisms. Pollination and seed dispersal are good examples of the maintenance interaction. These paths carry little of the system's energy but are essential for the maintenance of the ecosystem. Whitmore (1990) stressed these biological functions of interactions and called pollinators and seed dispersers the "mobile link species". Hence the numerical and functional aspects of a food web are two sides of a coin. More attention should be paid to the latter one. Therefore I focus on the functional aspect of the interactions in a tropical rain forest in this thesis.

A high proportion, typically 50-90%, of trees in tropical forests produce fleshy fruits (drupes, berries, and arillate forms) that are edible to a large number of frugivorous vertebrates (Fleming 1991). The term "frugivory" and "frugivorous" used here loosely refer to the widest meaning of the words, which includes both obligatory and opportunistic fruit consumption by animals. The year-round availability of fruit in tropical forests has led to the evolution of many specialized vertebrate frugivores. Both specialized and opportunistic frugivores are involved in a mutualistic exploitation system with their

food plants. To attract particular seed dispersers, plants have evolved a variety of fruit morphology, fruit color, chemical contents, and phenological strategies.

In this thesis, I deal with a community that consists of fruit-bearing plants and frugivorous mammals in a Malaysian tropical rain forest, the Pasoh Forest Reserve. There are roughly over 800 species of trees (Kochumen *et al.* 1990; Manokaran *et al.* 1992; Appanah & Weinland 1993) and 50 species of omnivorous-frugivorous mammals in the forest (Kemper 1988; Lim *et al.* 1995). The interactions concerned here are competition and reproduction within species and competition, predation, and mutualisms between species, all of which are influential in regulating or disturbing the population dynamics of constituent species in ecological time, and would act as important driving forces to evolve new behaviors, life histories, species, and interactions in evolutionary time. To understand the dynamics of the forest community based on these interactions, keystone species needs to be established.

The concept of "keystone species" is useful to understand the structure of a community in terms of the functional aspect of interactions. Plants bearing fruits throughout the year like *Ficus* spp. are the keystone species for many mammals and birds in some tropical rain forests (Terborgh 1986; Leighton & Leighton 1983; Lambert & Marshall 1991), because frugivores depend on the fruits of such plants as the baseline food during periods of food scarcity. Thus, one of the objectives in this thesis is to identify the keystone species of plants for frugivores in the tropical rain forest.

In order to understand the structure of the forest community, I discuss three ecological issues in relation to the temporal and spatial variations of fruit production: the habitat preference, frugivory, and population dynamics of small mammals. These are discussed in separate chapters. First of all, I describe the variation of fruit production and some environmental factors at the study site in time and space. Secondly, I discuss the variation of species composition of small mammals in different habitats, and their

environmental requirements. Thirdly, I discuss the food habits and community structure of frugivorous terrestrial mammals. Niche separation in food resources is an important mechanism for the coexistence of frugivores in some tropical forests (Fleming 1979; Gautier-Hion *et al.* 1985). Lastly, I discuss the population dynamics and reproductive ecology of small mammals. The significance of the bottom-up processes in the community is examined. My study is fully descriptive, and I believe that such a diversified description is one of the best ways to understand the functional aspect of the complex system of a tropical rain forest. All of the three ecological issues is discussed especially in relation to plant reproduction; namely the seasonal pattern of fruiting and the supra-annual cycles of "mast fruiting".

Mast fruiting is the most striking phenological feature in the aseasonal tropical rain forests of Southeast Asia (Foxworthy 1932; Burgess 1972; Medway 1972a; Janzen 1974; Appanah 1985; Ashton *et al.* 1988; Yap & Chan 1990). At irregular intervals of 2-10 years, a large number of plant species in a region come into flower in synchrony. Consequently, spectacular crops of seeds are produced and numerous seedlings are established within a short period.

Seed predation is considered to be an important factor in the evolution of this phenomenon. This is called the "predator satiation hypothesis (Janzen 1974)", where regionally synchronized mast fruiting at irregular intervals is an effective means of swamping seed predators, particularly in unproductive habitats that support low densities of seed predators during the long intervals between mast fruiting events.

The drastic change of food abundance in a mast fruiting event is expected to have a great impact on the population dynamics of frugivores. However, if animal abundance is limited by the bottom of food resources (Lack 1954), the fruiting condition of the normal years, not the mast fruitings, is critical for the population dynamics and species diversity of frugivores. Considering the short life cycles of small mammals, mast

fruitings would be less significant for their population recruitment. The question arises is how important the bottom-up processes in the frugivore community in the aseasonal tropical rain forests are. In order to answer this question, I conducted a long term study of the population dynamics of small mammals for a period covering a cycle from a normal period to a mast fruiting event. The present study is the first attempt to answer this question.

Lastly, I discuss the conservation of the mammalian community in the tropical rain forests of Malaysia in terms of the interactions between fruit-bearing plants and frugivores. The tropical rain forests of Peninsular Malaysia have been extensively diminished, fragmented, isolated, and degraded by human activities (Kiew 1991). Such circumstances cause the loss of species diversity of frugivores and the loss of the ecological processes they carry out. Consequently, this may lead to a crisis for the ecosystem. I also mention the importance of artificial treatments for logged forests in providing suitable habitats for frugivores and conserving viable populations of them.

Pasoh Forest Reserve

The study was conducted in the Pasoh Forest Reserve, Negeri Sembilan, Malaysia (latitude 2° 59'N, longitude 102° 19'E; altitude 75-150 m). The forest reserve was an inland forest with a broad expanse of flat lands and gently rolling ridges that adjoin the westward side of the Main Range of the Malay peninsula (Fig. II-1). The forest constituted about 2,500 ha of lowland mixed dipterocarp forests (Kochummen *et al.* 1990), including areas of primary and regenerating forests. The regenerating forest was selectively logged in the 1950s (Appanah & Mohd. Rasol 1990; Manokaran & Swaine 1994). The flora, forest structure, and other plant ecological issues have been described elsewhere (Kira 1978; Kochummen *et al.* 1990; Manokaran & Kochummen 1990; Manokaran *et al.* 1992). In total, 814 species of tree have been recorded in the 50 ha permanent plot established in the core area of the Pasoh Forest Reserve (Manokaran *et al.* 1992; Appanah & Weinland 1994). The mammalian fauna was described by Kemper (1988). She reported 84 species from 11 orders of mammals in the Pasoh forest.

Study area and study plot

A 10 ha (500 m x 200 m) study plot was established in the Southwestern part of the Pasoh Forest Reserve. Monthly trapping of small mammals, observation of fruit consumption by animals, monitoring of plant phenology, and several environmental surveys were carried out in the 10 ha study plot (hereafter the study plot). The surrounding area of the study plot covering about 100 ha of the forest was additionally used for a part of the observation of fruit consumption by animals using an automatic camera system.

The study plot was established in the boundary area between primary and regenerating forests. Its topography was generally flat and dry (Fig. II-2). As shown in Fig. II-3, the study plot consisted of three forest types; primary forest (hereinafter PF),

secondary forest (SF) and seasonally inundated area (SIA). They accounted for 43.2%, 22.4% and 34.4% of the study plot in area, respectively. PF was forest area where no anthropological disturbance was considered to have been undertaken. SF was regenerating forest that had been selectively logged in the 1950s (Appanah & Mohd. Rasol 1990; Manokaran & Swaine 1994). SIA was forest area with seasonal small streams. Its forest floor was covered with water in rainy seasons and occasionally dried up in dry seasons. I considered that a trapping site within 10 m of the edge of SIA belonged to the SIA habitat.

Climate

The Pasoh Forest Reserve was located in the driest part of Peninsular Malaysia (except for its northwestern part near South Thailand) where a more seasonal and less precipitation climate dominates (Dale 1959). Annual rainfall at Kuala Klawang, about 25 km west from the Pasoh Forest Reserve, was 1646 ± 32.0 SE mm on average for the period of 1963-1992, in the range of 1282-2256 mm/year (Malaysian Meteorological Services 1963-1992). Two dry seasons and two rainy seasons are clearly distinguished in a year (Fig. II-4). The bimodal pattern of rainfall is a characteristic for the western and the southwestern parts of the Malay peninsula, of which seasonality is generated by the monsoons (Dale 1959). The dry seasons are usually in January and July. Precipitation is sometimes below 100 mm/month.

The power spectrum of precipitation based on the monthly observations in Kuala Klawang over one hundred years is shown in Fig. II-5 (data source: Malaysian Meteorological Service). There are several peaks of frequency in rainfall cycles, at 0.5, 1, 2, 4-5, and 10 years. They are considered to be stable modes of climate, corresponding to the changes of monsoons, annual revolution of the earth, the Quasi Biennial Oscillation, the El Niño-Southern Oscillation, and more long-term cycles of climate change, respectively (Yasunari 1981; Inoue & Nakamura 1991; Inoue *et al.* 1993).

Chapter III. Meteorology, forest structure, and plant phenology
during the study period

Introduction

In this chapter, I describe the biotic and abiotic environmental factors in the study site during the study period. These are the meteorology, plant phenology, and forest structure; all of which are considered to influence the small mammal community.

Even in regions forming tropical rain forests, meteorological conditions fluctuate seasonally and inter-annually (Dale 1959; Yasunari 1981; Inoue & Nakamura 1991; Inoue *et al.* 1993), and the fluctuation strongly influences plant phenology (Whitmore 1984, 1990). The vertical and horizontal structure of forests provides the ecological niches for various kinds of animals (Harrison 1962). Therefore the details of these environmental factors are essential in order to discuss the ecology of small mammals in the forest.

Data sources and methods
Meteorological data sources

Three meteorological data sets were referred to. The first and the second were the meteorological observations using automatic weather stations carried out in the Pasoh forest by Saifuddin Sulaiman *et al.* (1994) for 1992-1993 and by Drs. Makoto Tani (Forestry and Forest Products Research Institute, Japan) and Abd. Rahim Nik (Forest Research Institute Malaysia) for 1994-1996 (Tani & Abd. Rahim Nik, unpublished data), respectively. The former was carried out at ground level (100 m above sea level; hereafter ground station) in an open area in the forest covered with grasses. The latter was carried out at the top level of an observation tower (52.6 m above the ground, 140 m above sea level), about 3 m above the highest tree crown nearby (hereafter tower-top station). The meteorological data observed at the meteorological stations in Pasoh Dua (5 km south from the Pasoh forest) and Kuala Klawang (25 km west) published by Malaysian Meteorological Service (1992-1994) were also referred to.

Forest structure and natural disturbances

(1) Vegetation survey

Two methods were used for the vegetation survey to describe the forest structure. In the first, five 20 m x 20 m quadrats were established randomly in each forest type, and diameters at breast height (dbh) of any trees (dbh $\geq$ 5 cm) were measured. In the second, locations of any large trees (dbh $\geq$ 60 cm) in the whole study plot were mapped and their dbh measured. Trees were not identified to species.

(2) Canopy gaps

The whole study plot was divided into 5 m x 5 m sub-quadrats (n = 400), and the canopy gap survey was carried out every year, in August 1992-1994, October 1995 and November 1996. A canopy gap was defined as a sub-quadrat where open sky ($\geq$ 10°) is seen over surveyor's head (1.5 m above the ground) at the center of the sub-quadrat. When any neighboring sub-quadrats around a gap were also judged as gaps, they were considered to constitute a continuous large gap. The gap size in area was a product of sub-quadrat size (5 m x 5 m) and the number of sub-quadrats constituting the gap.

(3) Fallen logs

The study plot was divided into 10 m x 10 m sub-quadrats (n = 100) and the number of fallen logs (diameter of the largest end $\geq$ 30 cm and $\geq$ 60 cm) was counted in February-March 1995.

Plant phenology

(1) Litter-trap method

Flowering and fruiting phenology were censused monthly from June 1992 to January 1997 using litter-traps. One hundred litter-traps, of which the open area was 0.5 m² each, were set systematically in a 2 ha area of the primary forest in the study plot.

Litter in the litter-traps was collected once a month in the middle of the month. The number of litter-traps that contained either flowers or fruits were recorded. The indices of flowering phenology (I_{flower}) and fruiting phenology (I_{fruit}) were given as the following equations:

$$I_{flower} = \frac{N_{flower}}{N_{total} - N_{disturbed}} \times 100 (\%)$$

and

$$I_{fruit} = \frac{N_{fruit}}{N_{total} - N_{disturbed}} \times 100 (\%),$$

respectively, where N_{total} and $N_{disturbed}$ represent the total number of litter-traps (i.e. 100 traps) and the number of disturbed litter-traps, respectively. N_{flower} and N_{fruit} indicate the number of litter-traps that contained any flowers or fruits, respectively. The number of disturbed litter-traps was small enough to be negligible through the study period. These phenological indices are considered to show the monthly fruit productivity in the primary forest habitat in an accumulative manner. The study period of plant phenology using litter-traps overlapped with the whole period of animal trapping using bananas as baits (Chapter IV).

(2) Line census method

Using a line census method, the distribution and abundance of fruits in the three forest types were censused monthly from October 1993 to April 1995, which overlapped for 19 months with the litter-trap census.

Three or four investigators walked along a fixed zigzag census route, which covers the whole 10 ha study plot. The distance between adjacent paths was 10 m. The

length of the census route was 12.2 km in total. Any fruits (diameter ≥ 0.5 cm) on the forest floor within 2 m from the census route were the subject for the study. Fruits were sampled and identified to species or genus, and the parent trees were mapped. Attributes of the fruit (size, weight, color, shape, and ripeness) were recorded. Abundance of the fruit was categorized into three grades: few, medium and abundant. They roughly represent 1-5 fruits/m^2, 5-10 fruits/m^2, and over 10 fruits/m^2 for medium-sized fruits, respectively.

Results

Climate

The climate during the study period is shown in Fig. III-1. Mean, maximum, and minimum air temperature and precipitation are shown. The observations at the tower-top station were discontinued in early 1995 due to difficulties with the measuring instruments.

The air temperature at the tower-top station was generally lower than that at the ground station. The minimum air temperature tends to be relatively lower in January-February than in the other months (Fig. III-1 a).

Annual precipitation in the Pasoh forest during the study period were 1560, 1710, 1510, and 2580 mm for 1992-1995, based on the data for the ground station. Generally, there were two short periods of less precipitation, early and in the middle of each year (Fig. III-1 b).

Forest structure

Forest structure of the three forest types is shown in Fig. III-2. For small to medium sized trees (dbh 5-60 cm), tree densities and basal areas of PF, SF and SIA were 1415, 1740, and 1820 trees/ha, and 32.3, 44.0, and 35.8 m^2/ha, respectively. The tree density of 5-10 cm and 10-15 cm dbh classes were higher in SF than in PF (Fig. III-2 a). Trees in these dbh classes in SF formed a mono-layered canopy at 10-15 m in height. In addition, SF had sparse understory and few saplings on the forest floor. For large trees

(dbh ≥ 60 cm), density of the 60-70 cm dbh class was higher in SF than in PF, while those in the other dbh classes were lower in SF than in PF (Fig. III-2 b).

Tree size distribution for SIA was similar to that for SF for small-medium sized trees (III-2 a) and to that for PF for large trees (Fig. III-2 b). SIA was quite bushy with many small trees (dbh < 10 cm). The small trees formed a dense leaf layer at 1-10 m in height. In addition, there were many respiratory roots on the forest floor in SIA.

Canopy gaps and fallen logs

Temporal change of canopy gap ratio and mean gap size in the three forest types are shown in Fig. III-3. The sudden rise of gap ratio and gap size in 1996, especially in PF, was caused by a heavy storm in late June 1995, when many large trees were uprooted and fell down involving neighbor trees. SF and SIA suffered little disturbance by the storm. The five-year average of gap ratio increased in the order SF (3.0 ± 1.75 SD %), PF (7.6 ± 4.73 SD %), and SIA (8.8 ± 2.27 SD %). The five-year average of mean gap size in PF, SF, and SIA were 95.8 ± 53.59 SD, 65.4 ± 47.05 SD, and 97.7 ± 37.45 SD m^2, respectively.

Distribution of fallen logs censused before the heavy storm is shown in Fig. III-4. Densities of fallen logs in PF, SF, and SIA were 27.6, 25.6 and 23.7 logs/ha for logs of diameter (d) ≥ 30 cm (Fig. III-4 a), and 14.1, 11.1 and 7.1 logs/ha for logs of d ≥ 60 cm (Fig. III-4 b), respectively. The density of large sized logs (d ≥ 60 cm) was higher in PF than in SF (G test, two-tailed, $p < 0.05$). When small logs (d ≥ 30 cm) were included, there was no statistical significance among forest types (G test, two-tailed, $p > 0.05$). Distributions of large sized logs and canopy gaps showed a positive correlation (r = 0.311, $p < 0.05$, Table III-1).

Flowering and fruiting phenology in the primary forest

Figure III-5 shows the density of fruiting trees in PF estimated by the two census methods. The estimation and their three-month moving averages are shown separately.

The trends were well coincident between the two methods and the correlation coefficients (r) were 0.550 and 0.844 for Figs. III-5a and b, respectively (p < 0.05 for both).

Figures III-6a & 7a show the flowering phenology monitored by litter-traps. There were two peaks of flowering in February-April and October. The former peak was dominant, while the latter was relatively weak. Flowering condition was normal in 1992-1995 and good in 1996 when a mass flowering occurred. The index of flowering (I_{flower}) was within the range of 0-17% in the normal years (mean 4.8 ± 4.27 SD %, n = 43), while that in 1996 increased sharply in March-April and reached a maximum (37%) in May 1996, then fell rapidly to 0% in August (Fig. III-6 a).

Fruiting showed less seasonality than flowering and fluctuated from year to year (Fig. III-6b & 7b). Normal fruiting years continued for the four years from 1992 to 1995 and was followed by a mast fruiting year in 1996. The index of fruiting (I_{fruit}) was within the range of 2-24% during 1992-1995 (mean 9.8 ± 5.85 SD %, n = 43). There were two long periods of fruit scarcity (three-month average of I_{fruit} < 10%, Fig. III-7b) in July 1993-April 1994 and November 1994-March 1996, and the latter lasted for 17 months. The index of fruiting in 1996 increased rapidly from May when immature fruits started to fall down and reached a maximum (I_{fruit} = 76%) in September when a large number of mature fruits were shed in synchrony (Fig. III-6 b).

The lag correlation between flowering and fruiting patterns is shown in Fig. III-8. There were positive correlations between these patterns, with lags of 2-5 months.

Phenology and fruiting species in the different forest types

The density of fruiting species and individuals censused by the line-census method are shown in Fig. III-9. Temporal patterns of fruiting were positively correlated between PF and SF (Table III-2). Correlation coefficients (r) between them were 0.816 for species and 0.706 for individuals (p = 0.004 and 0.031, respectively; after Bonferroni adjustment). There was no significant correlation between the fruiting patterns in SIA and the other two forest types (p > 0.05; after Bonferroni adjustment). The density of fruiting

individuals was higher in PF than in SF during the fruiting season (June-August 1994), while the density was nearly equal during the non-fruiting season (September 1994-August 1995, Fig. III-9 b).

Table III-3 shows the fruiting species found by the line census from May 1994 to April 1995. Species composition was different among forest types. The number of fruiting taxa found in PF, SF, and SIA were 47, 20, and 28, respectively, and they belonged to 29, 15, and 16 families, respectively. The dominant fruiting species in PF were in the genera *Dillenia*, *Eugenia*, *Garcinia*, *Ixonanthes*, *Knema*, *Ormosia*, *Ryparosa*, *Santiria*, and *Sarcotheca*. *Porterandia anisophylla* and *Styrax benzoin* were frequently recorded in SF. *Myristica cinnamomea*, *Myristica elliptica*, *Terminalia citrina*, and *Xerospermum noronhianum* were usually recorded in SIA. There was no significant difference in fruit size among forest types (Kruskal-Wallis test, p = 0.270).

Discussion

Forest structure

Using the diameter-height regression equation provided by previous studies in Pasoh (Kato *et al.* 1978; Kira 1978), the vertical structure of forest can be estimated from the dbh size distribution of trees. PF had a lower density of small trees and a higher density of large trees than SF (Fig. III-2a). The wide range of dbh size in PF indicates the well-developed vertical structure with multi-story canopies, whereas smaller variation of dbh in SF represents a mono-layered canopy at 10-15 m in height. Kira (1978) showed large trees (dbh ≥ 60 cm) compose the main and emergent canopy layers over 30 m in height in the Pasoh forest. The lower diameter limit of logging in the 1950s was 30 cm in dbh for commercial species (Appanah & Mohd. Rasol 1990). SF had fewer trees above 100 cm in dbh and more trees of 60-70 cm in dbh than PF (Fig. III-2b). This implies that SF consists of trees uniform in age and height and has less-developed vertical structures.

The ratio and size of canopy gaps were larger in PF than in SF (Fig. III-3). The distribution of large fallen logs was biased to PF, while such a tendency could not be

detected when small logs were considered (Fig. III-4). When the heavy storm hit the area in mid 1995, the canopy gap ratio of PF increased from 4.3% to 14.6%, while that of SF changed from 2.0% to 3.1% only (Fig. III-3). These suggest that SF provides a relatively low horizontal variation on the forest floor.

In contrast with the other forest types, SIA was bushy with a lot of small trees (Fig. III-2a). This implies that SIA has poorly developed canopy layers. The forest floor, which is seasonally covered with water, may provide unfavorable conditions for animals and inhibits their activities, especially in rainy seasons.

Plant phenology

In a tropical forest, Zhang & Wang (1995) compared the three census methods which are often employed to estimate fruiting phenology and fruit productivity, i.e. canopy observation from a platform, litter-traps, and ground survey. They found that any of them are applicable to approximate the annual fruiting phenology in terms of the number of fruiting species at the moment, and concluded that more than 80 traps are necessary for a correct record of the fruiting species richness by litter-trap method. The fruiting phenology monitored by the litter-traps and by the line census in this study are positively correlated (Fig. III-5), though the former indicates the amount of fruits in the forest in an accumulative manner, while the latter does so in instantaneous manner. Therefore, in this thesis, I use estimation by the litter-trap method as an index of plant phenology of PF.

The seasonal rhythms and inter-annual patterns of flowering and fruiting shown in Figs. III-6 & 7 agree with the results of previous work in some Malaysian forests. There are usually two flowering seasons and one main fruiting season in a year (McClure 1966; Medway 1972a; Wang 1982, 1986), and mast fruiting events occur at intervals of 2-10 years (Burgess 1972; Ng 1977; Ashton et al. 1988; Yap & Chan 1990). Since the previous mast fruiting event occurred in 1989 (LaFrankie & Chan 1991), the present study covered a period of four years of normal fruiting years and a subsequent mast

fruiting year. The consequences of the mast fruiting, especially in terms of its influence on the reproduction and population dynamics of small mammals, will be discussed in Chapter VI.

Fruit productivity

The distribution of fruit size was similar among the three forest types (Fig. III-10) and fruiting seasonality showed a positive correlation between PF and SF (Table III-2). However, higher fruit productivity in the fruiting season in PF (Fig. III-9) and a higher diversity of fruits there (Table III-3) suggests that this forest type provides a higher carrying capacity for frugivores.

On the other hand, the species richness of plants in SF is considered to have been reduced by the logging in the past. This may result in low fruit productivity in SF through a year (Fig. III-9), which provides for low carrying capacity of frugivores. Johns (1986) and Johns (1988) suggested that frugivores are seriously influenced by selective logging because their food supply is drastically reduced after logging.

In conclusion, PF tended to have more heterogeneity in time and space and higher fruit productivity. Thus PF may supply more suitable habitats to frugivores in comparison with the other forest types. The ecological differences, either biotic and abiotic, between PF and SF are thought to be an after effect of the logging carried out about 40 years ago. Since no artificial treatment has been done in the logged area after the logging (Manokaran & Swaine 1994), it is suggested that 40 years is still not enough for tropical rain forests to recover from the disturbance of selective logging.

Chapter IV. Distribution of small mammals and their habitat preference

Introduction

There have been previous works on mammalian communities carried out in Malaysian forests (Harrison 1957; Medway 1966, 1972b, 1978; Stevens 1968; Lim 1970a; Langham 1983; Duff *et al.* 1984; Kemper & Bell 1985; Payne 1985. Kemper 1988; Stuebing & Gasis 1989; Lim *et al.* 1995; Zubaid & Rizal 1995; Zubaid & M. Khairul 1997). Gathering the knowledge in literature together, one can tell something of the mammalian fauna in a certain habitat. However, most or nearly all these studies were fairly limited in their scope of community ecological concepts. Some were based on qualitative (presence/absence) information of species but not on quantitative aspects in terms of population density. Most studies dealt with only a fraction of the community; a few dominant species were studied but a number of rare species were ignored. There were some studies focusing on the comparison of mammalian fauna in different habitats, but they were carried out in study sites far away from each other. Furthermore, in most cases, the environmental conditions were too insufficiently described to discuss the factors regulating animal populations in the habitat.

The present study provides a more detailed discussion on the relationship between some environmental conditions and species abundance of small mammals, i.e. their habitat preference. Thirteen out of seventeen species in the small mammal community were subjected to statistical analysis. Several environmental factors described in Chapter III were considered.

Methods

Live trapping of small mammals

Two hundred and fifty animal live-traps were set systematically in a grid design on the forest floor in the 10 ha study plot. The distance between two adjacent traps was 20 m. The number of traps in PF, SF, and SIA were 108, 56, and 86, respectively. At

the center of the primary forest, there was a strip of regenerating forest (100 m x 20 m) that had been cut in early 1970s for a study of the International Biological Programe (IBP). This area is covered with secondary growth of 15-20 m in height at present. Animal traps were placed away from this area to minimize its effects.

Animal trapping was carried out monthly from June 1992 to January 1997. The size of traps was 17 cm x 17 cm x 44 cm, for width, height, and depth, respectively (made by Environmental Supplies and Services, Selangor, Malaysia). Fruit of the African oil-palm (*Elaeis guineensis*, family Palmae), which is widely planted as a crop in Malaysian plantations, was used as bait. One trapping session consisted of four consecutive days. The traps were checked once a day in the morning at 900-1300h.

An extended trapping session was carried out in July 1993, which consisted of ten consecutive days. For general analysis, the results in the first four days of the extended trapping session were used.

Animals captured were anesthetized with ether and toe-clipped individually for permanent identification. Each animal was identified to species according to the classification of Corbet & Hill (1992). At the initial capture of the individual, its body dimensions were measured as follows: Head and body (HB), tail (T), hind foot (HF) and ear (E) with a ruler (read to 1 mm), and body weight (*W*) on spring balances (read to 1 g for small species, 5 g for medium sized species, and 10 g for large species). Body weight was measured repeatedly for the first recapture of the month. Reproductive condition of individuals was examined and recorded at every recapture. The reproductive condition was classified into four categories for each sex: normal, slightly active, active, and very active for males according to the size of testis; and normal, pregnant, lactating, and post lactating for females according to appearance.

Data preparation

Four-year monthly trapping data from June 1992 to May 1996 was used for general statistical analysis (hereafter the main study period), because trap success rate was quite low in the mast fruiting period (Fig. IV-1).

Two data sets were compiled to analyze the spatial distribution of small mammal species: the number of captured individuals (hereafter *NI*) and the number of animal captures (hereafter *NC*). For example, if an individual is recaptured four times in a trapping session, *NC* takes it into account as four captures, while *NI* counts this as one individual.

Disturbance of animal traps was sometimes severe and different among habitats (Table IV-1). I employed two empirical regression equations to adjust for the effect of disturbance on the trapping data. The equations were derived from the results of the extended trapping session (Fig. IV-2). A saturating and a linear regression were applied to *NI* and *NC*, respectively. The regression equations obtained were

$$y = \frac{1.37x}{x + 891}$$

and

$$y = 0.000497x + 0.006,$$

respectively, where y is the accumulative ratio of the number of individuals or captures, and x is the accumulative number of effective traps; for instance, $x = 1000$ represents the total number of effective traps in a trapping session without disturbance. The coefficients of determination (r^2) for these regressions were 0.992 and 0.996, respectively.

Since the latter equation suggests that *NC* is directly proportional to the number of effective traps and its intercept was small enough to be negligible, the adjusted *NC* (n_{adj}) is given roughly by the equation

- 18 -

$$n_{adj} = \frac{n}{1 - D}$$

where n and D are the number of captures and the ratio of disturbed traps in a trapping session, respectively.

Statistical analyses

Two statistical methods were employed to reveal the bias of spatial distribution of small mammal species. One is based on the monthly NI of the species. If an individual was captured repeatedly among habitats in a trapping session, the individual was allocated among the habitats according to the frequency of captures. For instance, if an individual was captured twice in PF and once in SF and SIA, the probability of occurrence of the individual in each habitat was given as 2/4, 1/4, and 1/4, respectively. The summation of the probability for all the individuals in a habitat gives the monthly NI of the species in the habitat. The density of the species in PF, SF, and SIA were provided simply by the division of NI in the habitat by the area; 4.32, 2.24, and 3.44 ha, respectively. The density given by this method is used again for the analysis of population dynamics of small mammals in Chapter VI.

Another method is based on the accumulated NC at individual traps over four years. There was a strong edge effect on NC, as a greater number of animals were captured in the traps placed on the edge of the study plot. To reduce this edge effect, the outermost traps were excluded from the analysis. Thus, the number of traps in PF, SF, and SIA were reduced to 88, 40, and 56, respectively (184 traps in total). The linear model for the intensity of disturbance and NC described in the previous section was applied to the individual traps to adjust for the effect of disturbance. Then the arithmetical mean of NC for nine traps, i.e. one trap and its eight nearest neighbors, was calculated for all the traps except for those on the second outermost edge (n = 126). Square root

transformation was applied to *NC* plus 0.5 (Sokal & Rohlf 1996), and Pearson correlation coefficients (r) between species were calculated. Based on these correlation coefficients, the species occurrence patterns were classified using the unweighted pair-group method using arithmetic average (UPGMA). Furthermore, the correlations between the species occurrence patterns and the distribution of canopy gaps, small fallen logs (30 ≤ d < 60 cm), and large fallen logs (d ≥ 60 cm) were examined. SYSTAT for Macintosh (version 5.2.1) was used for the statistical tests and classification.

Ecological indices

An evenness index of species composition (*E*) known as the "modified Hill's ratio" (Ludwig & Reynolds 1988) was computed for the small mammal community of each habitat. This index is derived as

$$E = \frac{\lambda - 1}{e^{H'} - 1}$$

where *l* is Simpson's index and *H'* is the Shannon's index. Simpson's index is derived as

$$\lambda = \sum_{i=1}^{S} p_i^2$$

where *S* is the total number of species and p_i the proportional abundance of the *i*th species, given by

$$p_i = \frac{n_i}{N} \qquad i = 1,2,3,...,S$$

where n_i is the number of individuals of the ith species and N is the total number of individuals for S species in the community. Shannon's index is given by following equation.

$$H' = -\sum_{i=1}^{s}(p_i \ln p_i)$$

The index E varies from 0 to 1. E was chosen as the values are independent of the number of species in the sample and relatively independent of sample size. Consequently the values of E would not be affected by lower species richness (Ludwig & Reynolds 1988).

Results

Disturbance of traps

Traps were sometimes disturbed severely; in the worst case, the disturbance ratio reached nearly 50% of the total trapping effort (trap-days) in a habitat in a trapping session. Disturbance was considered to be chiefly made by *Macaca nemestrina* (the pig-tailed macaque). The ratio of disturbed traps was significantly different among the habitats, being 10.0%, 18.5%, and 15.9% for the four-year averages for PF, SF, and SIA, respectively (*G*-test, p < 0.001; Table IV-1).

Before adjusting for the effect of trap disturbance, the intensity of disturbance and the monthly *NI* correlated negatively, especially in SF (Fig. IV-3). The correlation coefficients in SF were statistically significant for the diurnal, nocturnal, and whole communities (r = -0.327, p = 0.023; r = -0.377, p = 0.008; and r = -0.424, p = 0.003, respectively; Table IV-2). After adjusting for the effect of trap disturbance, there were no significant correlations between the intensity of disturbance and *NI* in any cases (p > 0.1 for all the cases; Fig. IV-4 and Table IV-3).

Mammalian fauna exposed by the trapping

In total, 22 species of mammals belonging to eight families of six orders were recorded in the main trapping period. The most dominant order was Rodentia, including 8 spp. of squirrels, 5 spp. of rats, 2 spp. of flying squirrels, and 2 spp. of porcupines. Table IV-4 shows the body dimensions of the most dominant 17 species of small mammals with their locomotion and daily activity cycle. The number of species recorded in PF, SF, and SIA were 17, 15, and 15 species, respectively. Two species recorded only in PF were an arboreal squirrel (*Callosciurus prevostii*) and a flying squirrel (*Hylopetes spadiceus*). Except for some rarely captured species ($NI \leq 0.5$ individuals/month on average), 13 species of common small mammals were subjected to the analysis below. They were *Echinosorex gymnurus* (Echinaceidae, Insectivora), *Tupaia glis* (Tupaiidae, Scandentia), *Lariscus insignis*, *Callosciurus notatus*, *Callosciurus nigrovittatus*, *Rhinosciurus laticaudatus*, and *Sundasciurus lowii* (Sciuridae, Rodentia), *Leopoldamys sabanus*, *Maxomys surifer*, *Maxomys rajah*, *Maxomys whiteheadi*, and *Rattus tiomanicus* (Muridae, Rodentia), and *Trichys fasciculata* (Hystricidae, Rodentia).

Species composition among habitats

In this section, the results based on *NI* are shown. The density and biomass of the 13 species are shown in Tables IV-5 and IV-6. There were four remarkable differences in community structure among the habitats.

Firstly, total density and biomass decreased in the order PF, SF, SIA; four-year averages of 7.31 ± 1.89 SD, 5.43 ± 1.77 SD and 4.75 ± 1.36 SD ind./ha, respectively, and 1819, 1525, and 1369 g/ha, respectively (Table IV-5).

Secondly, the density of any diurnal species, including all the squirrels and *Tupaia glis*, were lowest in SF (Table IV-5). The density of the diurnal community was 3.13 and 2.43 ind./ha in PF and SIA, respectively, but only 1.18 ind./ha in SF. Diurnal squirrels and *Tupaia glis* accounted for 28.2% and 14.6% of the whole community in PF and 27.8% and 23.3% in SIA, while accounting for 8.5% and 13.2% in SF (Table IV-6).

On the contrary, the proportion of the nocturnal community was highest in SF (Table IV-6), in the order SF (78.3%) > PF (57.2%) > SIA (48.9%). The density of the nocturnal species was highest in SF (4.25 ind./ha), while densities of PF and SIA were 4.18 and 2.32 ind./ha, respectively (Table IV-5). This tendency resulted from the relatively high density of *Leopoldamys sabanus* in SF (2.62 ind./ha). The density of the nocturnal community in SIA was the lowest among the habitats. *Leopoldamys sabanus*, *Maxomys surifer*, and *Maxomys rajah* showed low densities; 1.30, 0.16, and 0.05 ind./ha, respectively.

Finally, the densities of *Echinosorex gymnurus* (moonrat) and *Trichys fasciculata* (long-tailed porcupine) among the habitats were highest in SIA; 0.31 and 0.10 ind./ha, respectively (Table IV-5). They accounted for 6.5% and 2.0% of the whole communities of SIA in density and 19.2% and 11.7% in biomass (Table IV-6).

As shown in Table IV-7, ten species of small mammals showed significant differences in population density among the habitats (Friedman test, $p < 0.05$ for all the ten species) and *Callosciurus nigrovittatus* showed marginal significance ($p = 0.052$). All the diurnal species and two species of rats, *Maxomys rajah* and *Maxomys whiteheadi*, showed higher densities in PF than in SF. On the other hand, densities of *Leopoldamys sabanus* followed the order SF > PF > SIA, while that of *Maxomys surifer* was of the order SF = PF > SIA. Density of *Echinosorex gymnurus* was higher in SIA than in PF.

The four-year average of E for PF, SF, and SIA was 0.785 ± 0.011 SE, 0.752 ± 0.014 SE, and 0.795 ± 0.011 SE, respectively. There was no significant difference among the habitats (Wilcoxon sign test, two-tailed, $p > 0.05$).

Guild composition among habitats

The 13 species of small mammals can be categorized into six ecological guilds according to their locomotion, daily activity cycle and food habit, as given by previous studies (Medway 1978; Payne *et al.* 1985). These are moonrats (*Echinosorex gymnurus*), treeshrews (*Tupaia glis*), rats (*Leopoldamys sabanus*, *Maxomys surifer*, *M. rajah*, *M.*

whiteheadi, and *Rattus tiomanicus*), terrestrial squirrels (*Lariscus insignis* and *Rhinosciurus laticaudatus*), arboreal squirrels (*Callosciurus notatus*, *C. nigrovittatus*, and *Sundasciurus lowii*), and porcupines (*Trichys fasciculata*). Guild composition of the three forest habitats based on *NI* are shown in Fig. IV-5. There were remarkable differences in guild composition among the habitats. The proportions of terrestrial and arboreal squirrels were small in SF as these guilds accounted for 4.7% and 3.8% of the total in SF, while accounting for 15.8% and 12.4% in PF and 17.1% and 10.7% in SIA. On the contrary, the proportion of rats was higher in SF (73.3%) than in PF (53.7%) and SIA (40.4%). Moreover, treeshrews occurred in a higher proportion in SIA (23.3%) than in PF (14.6%) and SF (13.2%).

Figure IV-6 shows the temporal changes of animal densities, guild composition, and guild evenness in the three habitats. The density of animals decreased in the order PF > SF > SIA (Fig. IV-6 a; Wilcoxon sign test, two-tailed, p < 0.016). The number of guilds was usually smaller in SF than the others, and the order was statistically confirmed as PF = SIA > SF (Fig. IV-6 b; Sign test, two-tailed, p < 0.001). Evenness largely fluctuated from month to month (Fig. IV-6 c). There were significant differences between any pairs of the three habitats, with the order SIA > PF > SF (Wilcoxon sign test, two-tailed, p < 0.001). The averages of guild evenness were 0.82 ± 0.01 SE, 0.72 ± 0.01 SE, and 0.65 ± 0.02 SE for SIA, PF, and SF, respectively.

Spatial distribution of species and environmental factors

In this section, the results based on *NC* are presented. Table IV-8 shows the correlation of spatial distribution between species. Absolute values of correlation coefficients (r) ranged from 0.001-0.757. Twenty nine out of 78 cases showed a significant positive correlation (p < 0.05, after Bonferroni adjustment), and 9 out of 78 cases showed a significant negative correlation (p < 0.05, after Bonferroni adjustment). Most of the significant negative correlations (6 of 9 cases) were associated with

Echinosorex gymnurus, *Trichys fasciculata*, *Leopoldamys sabanus*, *Maxomys rajah*, and *Maxomys surifer*.

Three clusters were recognized in the dendrogram of species occurrence patterns (Fig. IV-7). The first cluster was the largest, consisting of eight species. This cluster was divided into two sub-clusters. All the diurnal species except *Callosciurus nigrovittatus* constituted one sub-cluster, and the three species of rats (*Leopoldamys sabanus*, *Maxomys surifer* and *Maxomys rajah*) constituted another. The second cluster consists of *Callosciurus nigrovittatus* and *Rattus tiomanicus*. The third cluster consists of *Echinosorex gymnurus*, *Trichys fasciculata*, and *Maxomys whiteheadi*. The third was connected with the others by a negative correlation coefficient ($r = -0.135$).

Table IV-9 shows the correlation of spatial distribution between animal species and some environmental factors. *Leopoldamys sabanus* showed a negative correlation with canopy gaps ($r = -0.291$, $p < 0.05$, Bonferroni adjustment, $n = 126$). *Maxomys whiteheadi*, *Lariscus insignis*, *Rhinosciurus laticaudatus*, and *Sundasciurus lowii* showed a positive correlation with large fallen logs ($r = 0.295, 0.294, 0.379, 0.268$, respectively, $p < 0.05$ for all the cases, Bonferroni adjustment, $n = 126$).

Discussion

Grouping of small mammals according to their habitat preference

Stevens (1968) compiled the available information of the mammalian fauna in various habitats in Peninsular Malaysia and concluded that, in number of species, 18 out of 25 spp. (72%) of squirrels and 11 out of 26 spp. (42%) of rats were confined to primary forests. When including old secondary forests, the species found in natural forests account for 84% of squirrels and 65% of rats. Therefore, most of the Malaysian small mammals are considered to be forest dwellers.

The present study was generally consistent with this conclusion. Eight out of the 13 species (61.5%) showed significant preference for primary forest habitat over secondary forest habitat, and two species of rats (15.4%) tended to favor the secondary

forest habitat (Table IV-7). According to their habitat preference, the 13 species of small mammals can be categorized into four species groups; i.e. primary forest species, secondary forest species, water associated species, and ubiquitous species group (Table IV-10). The details of these species groups are as follows:

(1) Primary forest species group

This group consists of eight species. They are *Tupaia glis*, *Callosciurus nigrovittatus*, *Callosciurus notatus*, *Lariscus insignis*, *Rhinosciurus laticaudatus*, *Sundasciurus lowii*, *Maxomys rajah*, and *Maxomys whiteheadi* (Table IV-10). Their population densities were significantly higher in PF than in SF (Tables IV-5 & 7). This suggests that the primary forest habitat is more preferable for them than the secondary forest habitat. Comparing the population density in SIA with those in PF and SF, there was a difference between the diurnal and nocturnal species in this group. Treeshrews and squirrels (except *Sundasciurus lowii*) tend to prefer SIA to SF, while the reverse was shown for *Maxomys rajah* (Table IV-7). Distribution patterns for these diurnal species were highly correlated with each other (Table IV-8) and they formed a cluster (Fig. IV-7). Thus the habitat preferences of the diurnal species were in the order PF > (or '=' for some species) SIA > SF, while that of *Maxomys rajah* was in the order PF > SF > SIA. The habitat preference of *Sundasciurus lowii* and *Maxomys whiteheadi* were PF > SF, and there were no significant differences between SIA and the other two habitats.

(2) Secondary forest species group

This group consists of *Leopoldamys sabanus* and *Maxomys surifer* (Table IV-10). Their population densities were relatively higher in SF as well as in PF, and low in SIA (Table IV-5). The density of *Leopoldamys sabanus* was higher in SF than in PF, while that of *Maxomys surifer* did not differ significantly between the two habitats (Table IV-7). Thus the habitat preference of *Leopoldamys sabanus* and *Maxomys surifer* were in the order SF > PF > SIA and SF = PF > SIA, respectively. Both the primary and the

secondary forest habitats are considered to be preferable for them, while the basin area in the study plot where water covers its ground surface seasonally was avoided. This conclusion agrees with the findings of Harrison (1957) and Lim (1970a). These two species seem to be pre-adapted to disturbed environments.

(3) Water associated species group

This group is represented by *Echinosorex gymnurus* and *Trichys fasciculata* (Table IV-10). They showed a relatively higher density in SIA than in the other two habitats, though these species were captured in all the habitats in the study plot (Table IV-5). The population density of *Echinosorex gymnurus* was significantly higher in SIA than in PF (Table IV-7). This agrees with the findings of Lim (1967) and Medway (1978) that *Echinosorex gymnurus* is usually trapped near streams and prefers swampy forest. The population density of *Trichys fasciculata* tended to be higher in SIA than in the other two habitats (Table IV-7). Thus it can be concluded that these two species prefer wetter conditions on the forest floor. In addition, *Echinosorex gymnurus* and *Trichys fasciculata* showed similar distribution patterns (r = 0.524, Table IV-8) and belonged to the same cluster in Fig. IV-7.

(4) Ubiquitous species group

A medium-sized rat, *Rattus tiomanicus*, belongs to this group (Table IV-10). The species was captured in all the forest habitats in the study plot; population densities were 0.10, 0.10, and 0.12 ind./ha in PF, SF, and SIA, respectively (Table IV-5). This species seems to be influenced by neither logging disturbance nor the water conditions of the forest floor.

Potential factors affecting the distribution of small mammals

As small mammals have high mobility and the three habitats are adjacent to each other, there is no apparent obstacle for them to migrate among the three habitats.

Therefore the population density of a species in a habitat is expected to reach its equilibrium quickly if a disturbance is suffered. This is the view of the "ideal free distribution" proposed by Fretwell & Lucas (1970). Assuming that the ideal free distribution is achieved through an animal's habitat preference, I discuss potential factors determining population densities and distribution patterns of small mammals in different habitats.

(1) Primary forest species group

All the diurnal guild including treeshrews, arboreal squirrels, and terrestrial squirrels belong to this group (Table IV-10).

Firstly, I discuss the terrestrial squirrels, *Lariscus insignis* and *Rhinosciurus laticaudatus*. *Lariscus insignis* eats both plant and animal materials (Harrison 1961). The availability and diversity of fruits on the forest floor were higher in PF than in SF (Fig. III-9 & Table III-3). There is a positive correlation between fruit availability and population density of *Lariscus insignis* (Figs. VI-6 & 7; this issue will be further discussed in Chapter VI). Furthermore, *Lariscus insignis* nests in fallen trees or hollows under standing dead trees. There were more large fallen logs on the forest floor in PF than in SF (Fig. III-4 b). The captures of *Lariscus insignis* positively related to the existence of large fallen logs (Table IV-9). These suggest that the factors determining the population density of *Lariscus insignis* are resources for food and nesting.

Another ground squirrel, *Rhinosciurus laticaudatus*, is strongly insectivorous (Harrison & Lim 1950; Harrison 1961; Medway 1978). The biomass of ground invertebrates is larger in a primary forest than in an old secondary forest (Lavelle & Pashanasi 1989). The captures of *Rhinosciurus laticaudatus* were positively related to the existence of large fallen logs (Table IV-9). More large fallen logs in PF (Fig. III-4 b) may provide more foraging, hiding, resting, and nesting sites for terrestrial small mammals. These suggest that the factors determining the population density of *Rhinosciurus laticaudatus* are also resources for food and nesting.

Secondly, I discuss the arboreal squirrels in this species group, *Callosciurus notatus* and *Sundasciurus lowii*. They use the middle to lower stories of forest and sometimes search for food on the ground (Lekagul & McNeely 1977; MacKinnon 1978; Medway 1978; Whitten 1981; Payne *et al.* 1985). *Sundasciurus lowii* was mainly (82%) seen below 10 m in height (Whitten 1981), and *Callosciurus notatus* was most frequently observed (63%) below 15 m in height (MacKinnon 1978). Assuming that most individuals of these species are exposed to trapping, the carrying capacity of arboreal squirrels in PF seems to be higher than that in SF (Table IV-5). This may due to the higher density and species richness of fruiting trees (Fig. III-9 & Table III-3) and the well-developed vertical structure of the forest in PF (Chapter III).

Food and habitat structure may act as the principal determinants of the population density of other small mammals in this species group. The habitat preference for PF in other ground foraging species, such as *Maxomys rajah*, *Maxomys whiteheadi* and *Tupaia glis*, might be accounted for by these two factors because they are omnivorous, spend much time on the ground and nest in holes in fallen logs or underground (Medway 1978; Kawamichi & Kawamichi 1979; Langham 1982). The habitat preference for PF in another arboreal squirrel, *Callosciurus nigrovittatus*, might also be accounted for by those two factors, because the species is strongly frugivrous (MacKinnon 1978) and utilizes the highest part of the forest canopies (Tamura 1993; Tamura & Yong 1993). High fruit productivity (Fig. III-9 & Table III-3) and well-developed forest structure in PF may be preferable for *Callosciurus nigrovittatus*.

(2) Secondary forest species group

The two terrestrial rats in this group, *Leopoldamys sabanus* and *Maxomys surifer*, showed preference for disturbed forest habitat as well as undisturbed forest habitat (Table IV-7). They might not strongly depend on fallen logs as a resource for nests because they usually nest underground (Lim 1970a). This implies that these species can survive in disturbed forest habitats with less fallen logs.

(3) Water associated species group

  Echinosorex gymnurus has been known to prefer swampy forests or nearby streams as habitat (Lim 1967; Medway 1978). This species is said to depend on aquatic animals for food (Banks 1931; Davis 1962; Lim 1966, 1967; Gould 1978; Medway 1978), while Davis (1962) reported that the species feeds mainly on terrestrial invertebrates, such as earthworms, termites, beetles ,and other arthropods.

  A telemetric study revealed that *Echinosorex gymnurus* nests underground in dry places both in PF and SF, but not in SIA (Yasuda unpublished data). They have two or more nests and move among them frequently at intervals of several days.

  It is known that wild boars (*Sus scrofa*) intensively dig up the forest floor in wet areas near streams to search for food, probably earthworm (Kemper & Bell 1985; Payne *et al.* 1985). This implies that animal matters for food resources are potentially abundant in the surface soil in such a habitat. To maintain its large body, *Echinosorex gymnurus* may need to search for food over a large area, and the wet area near streams might be an important feeding site for the species.

  A telemetric study revealed that *Trichys fasciculata* nests underground in large fallen logs in dry places only (Yasuda unpublished data). Using an automatic camera system (this issue will be discussed in Chapter V), I found that *Trichys fasciculata* frequently comes to feed on fallen fruits on the ground in SIA as well as in PF and SF. Since the species had been caught also in SIA, it is quite probable that *Trichys fasciculata* utilizes such wet areas as a part of its feeding range. The large body size of *Echinosorex gymnurus* and *Trichys fasciculata* (Table IV-4) may allow them to forage about for food in wet areas, because they have a clear advantage in preventing heat loss in getting wet.

(4) Ubiquitous species group

  In contrast with the other rats, *Rattus tiomanicus* is captured in SIA as well as in dry forests, and its population density did not differ among habitats (Tables IV-5, 7 &

10). According to previous work, *Rattus tiomanicus* is a species usually found in cleared land, disturbed or fringing forest (Harrison 1958), but also occasionally in virgin forests (Medway 1972b). Harrison (1958) and Sanderson & Sanderson (1964) carried out their studies in grasslands and obtained the size of the home ranges of the species as 73-102 m and 120 m long, respectably. Although Harrison (1958) argued that *Rattus tiomanicus* has territoriality, my result did not concur. I captured 28 individuals in total during the four-year census, but most of them (89%) were caught only once. This suggests that, at least in the forest habitat, few individuals of *Rattus tiomanicus* settle their home ranges over several months and that they wander in the forest extensively.

Introduction

The mammal is a dominant component of the species assemblage of frugivores in Malaysian forests. Most of the mammals chiefly or partially depend on wild fruits for food (Harrison 1954, 1961; McClure 1966; MacKinnon 1978; Lim 1970a, 1993; Medway 1978; Payne 1980; Payne *et al.* 1985). Although there is a great deal of literature on the food habits of Malaysian frugivorous mammals, only a few studies provide a list of their food items at the species level, which allows us to discuss the species-species interactions between plants and animals and the guild structure in the frugivore community.

McClure (1966) studied fruit consumption by animals for 32 species of canopy trees from an observation platform above the canopy and recorded the fruit consumers of each fruiting tree. He found that arboreal mammals, namely giant squirrels (*Ratufa* spp.), gibbons (*Hylobates* spp.) and leaf monkeys (*Presbytis* spp.), are the common consumers of large fruits in the canopy, while various species of frugivorous birds are the consumers of small fruits on the tree. Payne (1980) compiled the observation records of frugivory made by some researchers in a Malaysian rain forest and presented a huge list of plants and their fruit consumers, which includes over 300 spp. of plants belonging to 53 families and 3 spp. of primates, 3 spp. of arboreal squirrels, and 6 families of frugivorous birds. He suggested that primates compete with squirrels and birds for fruits as food.

There are some difficulties in the previous studies to allow us to make a synthesis on the plant-frugivore interactions. One is that observations were made only in daytime for diurnal animals in the canopy, though many researchers mentioned that the consumption of fallen fruits was sometimes quite severe on the forest floor at night (McClure 1966; Payne 1980). Fruit consumption on the forest floor contributes to important ecological processes; not only seed predation but also seed dispersal (Gautier-

Hion *et al.* 1985; Forget 1990, 1992, 1993, 1994, 1996; Forget *et al.* 1994). Therefore all-day observation of the consumption of fallen fruits is needed.

Another point is that almost all the studies were not quantitative and were based on presence/absence information (binary data) of fruit consumers. A quantitative data set and statistical analysis are necessary to reveal the intensity of interactions and the structure of the community. So far Gautier-Hion *et al.* (1985) are the only ones who have applied a multivariate analysis to the fruit-frugivore interactions in a tropical rain forest. They studied 122 plant species and 39 species of both diurnal and nocturnal frugivorous vertebrates in a Gabonese forest, but they used presence/absence data of fruit consumers for each plant species. Gautier-Hion *et al.* (1985) suggested that fruit weight and color are the principal factors in determining the fruit choice of consumers and that there are two syndromes in fruit characters.

In the present study, I used an automatic camera system to carry out all-day observation of fruit consumption by vertebrates on the forest floor. An automatic camera system can provide quantitative data for fruit consumption as the number of photos of visiting animals, which allows us to apply some better statistical methods to describe the patterns of fruit-frugivore interactions in the tropical rain forest.

Methods

Automatic camera system

The automatic camera system consisted of a single-lens reflex camera (XR10-M with 35-70 mm zoom lens, RICOH, Japan), an infrared sensor (PS15-B, DELCATEC, Japan), a flash (Auto25SR, SUNPAK, Japan), and a battery. The details of the system are described in Miura *et al.* (1997). The infrared sensor, which detects the infrared rays radiated from an animal body, was hung from a rope about 1 m above the target fruits placed on the ground, and was connected to the camera with an electric cable. The camera had an auto-quartz timepiece, so that the time of each animal visit was printed on the photo. Each experiment was carried out just under the parent tree of the fruits. The

number of fruits placed under the sensor varied from 20 to 100. The length of each experiment depended on the fruit disappearance rate, however, each experiment was continued for at least one week. This study was carried out in an area including the 10 ha study plot for small mammal trapping and its adjacent area (about 100 ha in total), from July 1993 to May 1995 in the period of the normal (non mast-fruiting) years. In total, 108 plant individuals of 70 species of trees, shrubs, lianas, epiphytes, and rattans, belonging to 27 families were studied. Their locations were shown in Fig. V-1.

Ecological indices and statistical analyses

Although 108 individuals of 70 plant species were studied, only 71 individuals of 49 species for which the number of photos of visitors were 10 or more, were subjected to statistical analysis. According to my field observations, both cotyledon eaters and pulp eaters were recognized for two plant species. They were *Canarium littorale* and *Terminalia citrina*, fruits of which have a hard kernel enveloped in green leathery pulp. The cotyledon eaters are rodents (*Leopoldamys sabanus* and *Lariscus insignis*), and the pulp eaters are the others (*Macaca nemestrina*, *Tragulus javanicus* and others). Therefore, the cotyledons and the pulp of those fruits were analyzed separately; hereafter I call them by their scientific name plus either cotyledon or pulp. Rattans (*Daemonorops* spp.) were difficult to identify to species, so they were considered as one taxon.

Three statistical methods of community ecology were employed to analyze the same data set obtained by the automatic camera experiments. The first is the similarity index of species composition, Morisita's similarity index C'_λ (Morisita 1959, 1971). This index represents the degree of average overlap between communities based on all the possible combinations of two components in the communities. The index was chosen as its values are relatively independent of sample size (Kobayashi 1995). C'_λ between two communities of j and k is derived as

$$C_\lambda = \frac{1}{\overline{\lambda}_g} \frac{\sum_i n_{ij} n_{ik}}{N_j N_k}$$

where $\overline{\lambda}_g$ is given by the equation of

$$\overline{\lambda}_g = \frac{\sum_i n_{ij}(n_{ij}-1) + \sum_i n_{ik}(n_{ikj}-1)}{N_j(N_j-1) + N_k(N_k-1)}$$

where N_j and N_k are the total abundance of the jth and the kth communities, respectively, and n_{ij} and n_{ik} are the abundance of the ith species in the jth and the kth communities, respectively. The values of Morisita's similarity index and dendrograms were computed by a computer program MULVAC'95 (Kobayashi 1995).

The second is the Two-way Indicator Species Analysis (TWINSPAN) proposed by Hill (1979a). This is a classification method that uses the divisive (top-down) strategy, whereas most classification methods including Morisita's similarity index employ the agglomerative (bottom-up) strategy (Kobayashi 1995). TWINSPAN is relatively robust against the random error of samples and leads to very interpretable solutions (Gauch 1982; Jongman *et al.* 1995; Kobayashi 1995). To make a dichotomy, TWINSPAN uses a set of indicator species that are derived from the partitioning of the first axis of the Correspondence Analysis (CA). In the present study, TWINSPAN was used to construct an ordered two-way table from the fruit-frugivore interaction matrix. The cut-off levels were set as 0-5%, 5-10%, 10-20%, 20-50%, and more than 50% in relative abundance of the animal species in number of photos. TWINSPAN was executed by a TWINSPAN program (Hill 1979a) in Cornell Ecology Programs.

The third is the Detrended Correspondence Analysis (DCA) proposed by Hill (1979b) and Hill & Gauch (1980). DCA is an ordination method and its solution is interpretable for both communities of plants and animals in the present study. DCA was

executed by MULVAC'95 (Kobayashi 1995), which is based on the program by Hill (1979b).

Nutrient analysis

Nutrient analysis was carried out for 24 edible parts of 21 selected species belonging to 15 families. Most of them showed a high rate of fruit disappearance or shed the fruits at high density levels on the forest floor. The nutrients analyzed were moisture (W), crude protein (CP), crude fat (EE, called after ether extract), crude fiber (CF), and ash (Ash). Nitrogen free extract (NFE), which represents carbohydrates (starch and sugar), was calculated as the residual fraction of the contents. Gross energy (GE, kcal/100 g in dry matter) was calculated from the equation of

$$GE = 5.61 \times CP + 9.66 \times EE + 4.38 \times NFE + 5.06 \times CF.$$

The procedures and machines used for the nutrient analyses are described below.

Dry matter (DM):

Specimens were dried in a dryer (105 °C) until a final weight was obtained.

Crude protein (CP):

Crude protein was given as the product of 6.25 and nitrogen content obtained by Kjedahl method. Vapodest (made by Gerhardt, Germany) was used.

Ether extract (EE):

Specimens were boiled in petroleum benzoin (60-80 °C) for 7-8 hours. The balance between before and after the procedure gives EE. Soxtherm (made by Gerhardt, Germany) was used.

Crude fiber (*CF*):

The residual fraction after extraction with H_2SO_4 and KOH was ashed. The balance between before and after the procedure gives *CF*. Fibertec system 1010 Heat Extractor (made by Tecator, Switzerland) was used.

Ash:

Specimens were kept in furnace (500 °C) for 8-16 hours and weighted.

Results

Frugivores exposed by the automatic camera system

The plant species treated in this thesis (70 spp.) were scattered among various families (Fig. V-2), and accounted for 8.6% of 814 known species in the Pasoh 50 ha plot (Manokaran *et al.* 1992). The families Euphorbiaceae, Myristicaceae, Moraceae, and Fagaceae were studied intensively, because the species belonging to these families bore fruits more frequently during the study period. However the family Dipterocarpaceae is a dominant component of the Pasoh forest (Kochummen *et al.* 1990; Manokaran & Kochummen 1990; Manokaran *et al.* 1992; Appanah & Weinland 1993), but only 4 spp. of the family were studied because the study period did not include any mast fruiting events.

Nearly 4000 photos of animals were taken, and 34 spp. of animals were identified. They belonged to various taxa, including the class Mammalia, Aves, and Reptilia. The most dominant class was Mammalia, including the order Pholidota (1 sp.), Insectivora (1 sp.), Scandentia (1 sp.), Chiroptera ($\geq$ 1 spp.), Primates (2 spp.), Carnivora (5 spp.), Artiodactyla (2 spp.), and Rodentia (11 spp.). All the terrestrial small mammals captured by the animal trapping (Table V-4) were recorded.

Forty nine species, plus two edible parts of fruits, and 16 species of the most popular frugivores were subjected to the analysis. The assemblage of frugivores consisted

of 13 spp. of Mammalia, 2 spp. of Aves, and 1 sp. of Reptilia (Table V-1). *Macaca nemestrina* (pig-tailed macaque) was the most common visitor by numbers of photos and utilized 44 out of the 49 plant species (89.8%, Table V-1). The second most common animals were the small mammals that were also commonly trapped (Chapter IV). *Leopoldamys sabanus*, *Lariscus insignis*, and *Maxomys* spp. utilized 26 out of the 49 plant species (53.1%). *Maxomys* spp. represents either *Maxomys rajah* or *Maxomys surifer*, which were unable to be distinguished in the photos. The ungulates, *Sus scrofa* (wild boar) and *Tragulus javanicus* (lesser mouse-deer), were also recorded, and utilized 15 (30.6%) and 14 (28.6%) spp. of the fruits, respectively. *Prebytis femoralis* (banded leaf monkey) consumed 4 spp. (8.2%) of the fruits. Although several species of birds were recorded in this study, only *Lophura erythropthalma* (crestless fireback) and *Chalcophaps indica* (green-winged pigeon) were common and utilized 6 and 2 spp. of the fruits, respectively. Water lizards, *Varanus* spp., were also common and utilized 15 spp. (30.6%) of the fruits.

Daily activity cycles of frugivores

Daily activity cycles of several common species are shown in Fig. V-3, based on the visiting time printed on the photos. Three activity cycles were recognized. The first was diurnal represented by *Macaca nemestrina*, *Lariscus insignis*, and *Tupaia glis*. The second was nocturnal including *Leopoldamys sabanus*, *Maxomys* spp., and *Trichys fasciculata*. The last was the non-circadian consisting of the two ungulates, *Sus scrofa* and *Tragulus javanicus*.

Classification of plant individuals using Morisita's similarity index

Table V-2 shows the fruit-frugivore interaction matrix of plant individuals by animal species by number of photos (hereafter the individual data). Using Morisita's similarity index, 73 plant individuals, including two edible parts of *Canarium littorale* and *Terminalia citrina*, of 49 species were classified (Fig. V-4, Table V-3). Five clusters are

recognized. They are named after the most dominant species of frugivore on average: the clusters *Macaca* (including 43 ind. of plants), *Lariscus* (7 ind.), *Leopoldamys* (9 ind.), *Presbytis-Hystrix* (3 ind.), and *Trichys* (11 ind.). The plant individuals belonging to each cluster are shown in Table V-3. Note that the plant individuals classified into the same cluster do not always contain the first most dominant species of animals, because the overall similarity of frugivore occurrence between fruits is concerned with progressing agglomeration.

In the cluster *Macaca*, *Macaca nemestrina* accounted for 56.6% of the photos on average (Table V-3). Other dominant species were *Tupaia glis* (8.2%) and *Leopoldamys sabanus* (6.6%). This cluster is divided into three subclusters, according to the composition of consumers. The subcluster *Macaca* (including 23 ind. of plants) was strongly predominated by *Macaca nemestrina* (66.1% on average). Note that the two individuals of *Sarcotheca monophylla* were not consumed by *Macaca nemestrina* but by *Lophura erythrophthalma* (46.7% and 44.8%, respectively). The subcluster *Leopoldamys* (14 ind. of plants) is predominated by *Leopoldamys sabanus* (10.4%) and *Tragulus javanicus* (9.1%), except for *Macaca nemestrina* (54.1%). In the subcluster *Tupaia* (6 ind.), here the most dominant species changed to *Tupaia glis* (52.4%), and others were *Macaca nemestrina* (20.5%), *Leopoldamys sabanus* (10.5%) and *Lariscus insignis* (8.5%). *Sapium baccatum* is not in the three subclusters shown above, which was predominated by *Chalcophaps indica* (75.0%).

The cluster *Lariscus* was predominated by *Lariscus insignis*, which accounted for 59.9% of the photos on average, and other remarkable consumers were *Maxomys* spp. (16.7%).

The fruits in the cluster *Leopoldamys* were mainly consumed by *Leopoldamys sabanus*, which accounted for 65.3% of the photos on average. Other dominant consumers were *Macaca nemestrina* (10.3%) and *Lariscus insignis* (9.5%).

The cluster *Prebytis-Hystrix* consisted of the three fruits: *Castanopsis megacarpa*, *Horsfieldia sucosa*, and *Lithocarpus ewyckii*. The former two were severely consumed

by *Prebytis femoralis*, while the rest was mainly consumed by *Hystrix brachyura*. This cluster connected with the cluster *Leopoldamys* at the next step of the classification, and then connected with the cluster *Macaca* (Fig. V-4).

The cluster *Trichys* was quite dissimilar from the other clusters ($C'_\lambda = 0.223$, Fig. V-4). The plant species in the cluster belonged to a variety of families: Flacourtiaceae, Guttiferae, Lauraceae, Leguminosae, Meliaceae, Myristicaceae, and Myrtaceae. *Trichys fasciculata* (long-tailed porcupine) was the most predominant consumer of these fruits, in the range 26.4-95.7% of the total photos. The second remarkable consumer in the cluster was *Hystrix brachyura* (common porcupine), which accounted for 10.9% of the total photos. The cluster *Trichys* is designated as "porcupine favored fruits".

Classification of plant species using Morisita's similarity index

The number of photos was summed up for all the replications of the same species to compose the interaction matrix of plant species by animal species (hereafter the species data). Figure V-5 and Table V-4 show the result of the classification using Morisita's similarity index. The structure of the species dendrogram was quite similar to that of the individual dendrogram and simpler. Five clusters were also recognized, and the most dominant animal species in these clusters were unchanged; they are the clusters *Macaca* (including 29 spp. of plants), *Lariscus* (3 spp.), *Leopoldamys* (5 spp.), *Presbytis-Hystrix* (3 spp.), and *Trichys* (11 spp.). The four plant species of which replications showed low similarity between them in the classification of individuals above were integrated into the clusters *Macaca* (*Baccaurea parvifolia*, *Xerospermum noronhianum*, and rattan) and *Lariscus* (*Sarcotheca monophylla*).

In the cluster *Macaca*, *Macaca nemestrina*, *Tupaia glis*, *Leopoldamys sabanus*, and *Lariscus insignis* occupied 57.3%, 7.4%, 7.1%, and 6.4% of the total photos on average, respectively. Here the cluster *Macaca* was more monotonous than that in the classification based on the individual data and contained no subclusters in it (Fig. V-5). The cluster *Presbytis-Hystrix* consisted of the three plant species that had been classified

into the same cluster by the individual based analysis. The cluster *Trichys* was most dissimilar among the plant assemblage.

As shown in Fig. V-6, the number of consumers recorded varied among plant species, in the range 1-12 spp. (mean = 4.7 ± 0.315 SE, median = 4, mode = 4). The most favored species was *Sarcotheca monophylla* (Oxalidaceae), which bears red juicy fruit, and was consumed by 12 spp. out of the 16 animal species. *Archidendron bubalium* (Leguminosae) and rattan (Palmae) were the second most favored species and were eaten by 9 spp. of animals.

Classification of animal species using Morisita's similarity index

The dendrograms of animal species derived from the individual and species data matrixes were similar to each other (Figs. V-7 & 8). Two clusters were recognized in both cases. One larger cluster consisted of *Macaca nemestrina*, *Sus scrofa*, *Maxomys* spp., *Hystrix brachyura*, *Lophura erythropthalma*, *Rhinosciurus laticaudatus*, *Varanus* spp., *Tragulus javanicus*, and *Tupaia glis*. Another cluster consisted of *Leopoldamys sabanus*, *Rattus tiomanicus*, and *Maxomys whiteheadi*. The former contained various animal species in taxa and body size, while the latter consisted of three species of nocturnal rats. In addition, *Trichys fasciculata* showed the least similarity in fruit utilization in the animal assemblage. This species was connected with the others at 0.098 and 0.125 in Morisita's similarity index based on the individual and the species data, respectively.

Classification using TWINSPAN based on the individual data

The result of TWINSPAN based on the individual data is presented as an ordered two-way table (Table V-5). The numerals in the table indicate the relative abundance of the animal species in number of photos; 1, 2, 3, 4, and 5 represent 0-5%, 5-10%, 10-20%, 20-50%, and more than 50%, respectively ('-' represents absence of the species). The individual number of plants in Table V-5 corresponds to that in Table V-6. The plant

individuals were divided into four groups (Table V-5). The former two groups (A and B) and the latter two groups (C and D) were divided at the first step of dichotomy. The indicator species at the first dichotomy were *Lariscus* (abundance level ≥ 2), *Macaca* (≥ 4), *Leopoldamys* (≥ 2), and *Tupaia* (≥ 1) for the groups A and B, and *Trichys* (≥ 2) and *Hystrix* (≥ 1) for the groups C and D. At the next dichotomy, the indicator species between the groups A and B was *Macaca* (≥ 3), and that between the groups C and D was *Presbytis* (≥ 1). Furthermore, group C was divided into two subgroups C1 and C2, according to the presence of *Trichys* (≥ 4) for C1 and *Macaca* (≥ 4) for C2, respectively.

Classification using TWINSPAN based on the species data

The result of TWINSPAN based on the species data is shown in Table V-7. The same cut-off levels of animal abundance described previously were used. Plant species were also divided into four groups. The former two groups (A and B) and the latter two groups (C and D) were divided at the first step of dichotomy. The principal indicator species between the groups A and B were *Lariscus* (abundance level ≥ 2) and *Leopoldamys* (≥ 4), and between the groups C and D was the presence of *Presbytis* (≥ 1). Furthermore, group C was divided into two subgroups C1 and C2, according to the presence of *Macaca* (≥ 4) for C1 and *Trichys* (≥ 4) for C2, respectively. The plant species classified into the groups or subgroups are shown in Table V-8. Generally, the groups A, C2, C1, and D in Tables V-5 & 6 corresponded to the groups A, C1, C2, and D in Tables V-7 & 8, respectively. The components of the group B in Table V-6 were classified into several groups in Table V-8.

Comparison between the two classification methods

Tables V-9 & 10 show the comparison between the results of the two classification methods for the individual and species data sets, respectively. Asterisks indicate disagreements between the two classification methods, which indicates individuals or species which were categorized into the non-corresponding groups using

TWINSPAN. These were 10 individuals (13.7% of 73 individuals, Table V-9) and 12 species (23.5% of 51 species, Table V-10), respectively. Asterisks in parentheses in the cluster *Macaca* (Table V-10) are not taken into account, because TWINSPAN is sensitive to the indicator species but less sensitive to the most common species such as *Macaca nemestrina*. In general, the results of the two classification methods showed a good agreement with each other, 86.3% and 76.5% for individuals and species classification, respectively.

Ordination of animal and plant communities

Based on the species data matrix, 16 animal species and 49 plant species plus 2 edible parts were ordinated using DCA. Eigenvalues of the first and second axes were 0.753 and 0.380, respectively.

For the animal species assemblage, the diurnal and nocturnal species were scattered separately in the DCA plane (Fig. V-9). The diurnal species dispersed on the lower right, while the nocturnal species were scattered on the upper left in the plane. *Macaca nemestrina* was located in the center. *Tupaia glis*, *Lariscus insignis*, and *Tragulus javanicus* were found at the bottom of the plane. The three species of rats, *Maxomys whiteheadi*, *Rattus tiomanicus*, and *Leopoldamys sabanus*, were at the uppermost, and the two species of porcupines, *Trichys fasciculata* and *Hystrix brachyura*, were at the furthest left in the plane. *Chalcophaps indica* (emerald dove) was on the extreme right and far from the others.

For the plant species, the species belonging to the six popular families and the others are shown in separate figures (Fig. V-10). The species in the families Burseraceae and Combretaceae and those in the families Dipterocarpaceae and Fagaceae are shown in the same figures, respectively, because these fruits are morphologically similar.

Most plant species were found in the center of the DCA planes (Fig. V-10). *Sapium baccatum* (Euphorbiaceae), which is a pioneer species bearing green-purple juicy fruit, was located on the extreme right of the DCA plane of plants, corresponding to the

position of its dominant consumer *Chalcophaps indica* on the DCA plane of animals (Fig. V-9). Some species of Myristicaceae (*Knema hookeriana*, *Myristica cinnamomea*, and *Myristica elliptica*), Leguminosae (*Archidendron bubalium* and an unknown sp.), Guttiferae (*Garcinia nervosa*) and Meliaceae (*Dysoxylum acutangulum*) were out of the center and made a clump on the extreme left of the DCA plane of plants, corresponding to the locations of their dominant consumers *Trichys fasciculata* and *Hystrix brachyura* on the DCA plane of animals (Fig. V-9). The cotyledon was always higher than the pulp of the same species in *Canarium littorale* (Burseraceae) and *Terminalia citrina* (Combretaceae).

Nutrient contents of fruits

The plant species subjected to the nutrient analysis were well scattered in the DCA plane of plants (Fig. V-11). Nutrient contents and gross energy of 24 edible parts of 21 fruits are shown on both a fresh matter and dry matter basis (Table V-11). Nutrient contents varied widely among fruits: Moisture 8.8-90.5%, Protein 1.6-33.7%, lipid 0.1-78.3%, and carbohydrate 1.2-93.9% on a dry matter basis. The gross energy was estimated in the range of 4347-8650 cal/g on a dry matter basis.

Nutrient contents and animal preferences

The long-tailed porcupine (*Trichys fasciculata*) showed a high preference for some particular fruits (Tables V-3, 4, 6 & 8). Table V-12 shows the eight species which were categorized into the corresponding categories of *Trichys* using Morisita's similarity index and TWINSPAN (hereafter porcupine-favored fruits). They were *Knema hookeriana*, *Myristica cinnamomea*, and *Myristica elliptica* (Myristicaceae), *Archidendron bubalium* and an unknown species of legumes (Leguninosae), *Garcinia nervosa* (Guttiferae), *Dysoxylum acutangulum* (Meliaceae), and *Beilschmiedia madang* (Lauraceae). *Trichys fasciculata* was the first or the second most frequent consumer of these fruits and accounted for 26.2-95.7% of the photos.

The porcupine-favored fruits are rich in nutrient and energy (Table V-13). *Archidendron bubalium* contained 7.0% of protein on a fresh matter basis (16.1% on dry matter basis), which is the second highest value among the fruits surveyed. The other five edible parts of the four porcupine-favored fruits were rich in lipid, in the range 6.7-55.0% on a fresh matter basis (15.1-78.3% on dry matter basis). The lipid content of the porcupine-favored fruits is significantly higher than that of the other fruits (Mann-Whitney's U-test, two-tailed, $p = 0.006$). There was no significant difference between the porcupine-favored fruits and the other fruits in the other nutrients (Mann-Whitney's U-test, two-tailed, $p > 0.1$). Mean gross energy of the porcupine-favored fruits was 3297 ± 653 SE cal/g on fresh matter basis, while that of the other fruits was 1841 ± 355 SE cal/g. The porcupine-favored fruits contained significantly higher energy in unit weight than the others (t-test, two-tailed, $p = 0.033$).

Fruit color and animal preferences

Fruit color was divided into two categories, green and colored. The latter consisted of fruits of either yellow, orange, brown, red, purple, black, or white. Fruit color at time of consumption by animals was under consideration. For example, *Lithocarpus* spp. and *Castanopsis megacarpa* were categorized into the green fruits, because they are severely eaten by monkeys and rodents before they ripen to brown. For dehiscent fruits, the color of inner part of the fruits displayed for animals was considered. For example, *Xylopia malayana*, of which the outer and inner colors are green and red was considered as a colored fruit.

All frugivores did not show a significant preference for colored fruits (Mann-Whitney's U-test, two-tailed, $p > 0.3$), except for water lizards, *Varanus* spp. (Mann-Whitney's U-test, two-tailed, $p = 0.040$). On the other hand, *Hystrix brachyura* and *Tragulus javanicus* showed a significant preference for green fruits (Mann-Whitney's U-test, two-tailed, $p = 0.008$ and 0.035, respectively).

Correlation between fruit characters and the first and the second axes of DCA plane

The energy content of the 17 fruits were plotted against the scores of the first axis of the DCA plot (Fig. V-12). There was a significant negative correlation between them (r = 0.506, p < 0.05). The cotyledon of *Canarium littorale* was eliminated from the calculation, because the cotyledon is protected by a hard kernel so that only a few particular animals can utilize it. The other nutrients were also plotted against the scores of the first DCA axis (Fig. V-13). Correlation coefficients (r) between them were -0.423, -0.640, 0.321, and 0.345 for protein, lipid, carbohydrate, and moisture, respectively. There was a significantly negative correlation for lipid (p < 0.05) and a marginally negative correlation for protein (p < 0.1).

Next, Fig. V-14 shows the relationship between the morphological protection of the fruits and the scores of the second DCA axis. Protected fruits indicate fruits that have any morphological mechanisms, namely a hard husk, thick rind, or spines enveloping their edible parts. The scores of the second axis of protected fruits were significantly greater than those for unprotected fruits (t-test, p = 0.049). The size of fruits were not related to the scores of the second DCA axis (Kruskal-Wallis test, p = 0.193)

Discussion

Robustness of the classification

Experiments using the automatic camera system were carried out under different conditions in time and space; for example, the population densities of animals varied among vegetation (in Chapter IV) and fluctuated temporally (in Chapter VI). Thus a question arises as to how robust the obtained classifications are. In this section, I examine several factors that may potentially influence the similarity index and its classification, and discuss the limitations of the study method.

(1) study period

There were five replications carried out in different periods for the same plant individuals (Table V-14). The values of Morisita's similarity index between them were relatively high, in the range of 0.572-1.116. This suggests that the experiments carried out in different periods for the same tree tend to give similar results.

(2) location of individuals

There were six replications carried out for different individuals of the same species in the same vegetation (Table V-14). *Baccaurea parvifolia* and *Sarcotheca monophylla* showed low similarity between the replications ($C'_\lambda < 0.5$). It is necessary to point out that the pairs of individual nos. 60 and 61, and nos. 62 and 63 of *Sarcotheca monophylla* represent the same individuals in different periods. The similarity of the former pair was low ($C'_\lambda = 0.310$), whereas that of the latter was high ($C'_\lambda = 0.751$). This suggests that it is not always true to say that "the experiments carried out in different periods for the same tree tend to give similar results". Further examination is needed.

(3) vegetation

Except for some cases, the values of the similarity index between replications were high, even though the experiments were carried out in different vegetation for the same species (Table V-14). Indices for *Canarium littorale* (pulp), *Porterandia anisophylla*, and *Pyrenaria acuminata* were 1.000 or more. This suggests that the vegetation does not always strongly influence the results. This is quite surprising because population densities and species composition of small mammals differed among different vegetation as discussed in Chapter IV.

There are three possible factors to reduce the effect of differences in species composition among habitats. First, the population density of a few common species are similar among habitats, namely *Leopoldamys sabanus* (Tables IV-5, 6 & 7) and *Macaca nemestrina* (Lim *et al.* 1995). Secondly, consumers at low population density are likely to

be photographed if they exist around the fruiting tree. Since the fruit availability is usually low in normal years (Chapter III), frugivores might come to feed on whatever they can accept in their home ranges. Finally, animal species having strong preference for some particular fruits, e.g. *Trichys fasciculata* (Table V-12), are likely to be photographed. This may be because the porcupine-favored fruits, *Archidendron bubalium* and *Myristica elliptica*, showed high similarity between replications (Table V-14).

(4) Competition among consumers

Low similarity between replications occurs when either *Lariscus insignis* or *Tupaia glis* occupies a large proportion of the photos. For example, *Lariscus insignis* accounted for 81.6% of the photos in a replication of *Sarcotheca monophylla* (no. 60), and *Tupaia glis* accounted for 43.2% of the photos in another replication (no. 61). In the classification using Morisita's similarity index they were classified into the cluster *Lariscus* and the cluster *Macaca* subcluster *Tupaia*, respectively (Table V-3, Fig. V-4). The same tendency was also found in *Xerospermum noronhianum* (C'_λ = 0.302). *Lariscus insignis* accounted for 50.0% of the photos in a replication (individual no. 72), while *Tupaia glis* accounted for 62.5% in another (individual no. 71). These plant individuals were classified into the cluster *Lariscus* and the cluster *Macaca* subcluster *Tupaia*, respectively (Table V-3, Fig. V-4). The dissimilarity between the replications in *Sarcotheca monophylla* and *Xerospermum noronhianum* may partially result from the competition between *Lariscus insignis* and *Tupaia glis*. They are common in the Pasoh forest (Tables IV-5 & 6) and spend much time on the ground in daytime (Kawamichi & Kawamichi 1979; Langham 1982), and are considered to have overlapped food habits (Harrison 1961). The two plant species above are similar in fruit characters. Firstly, their fruits have soft edible parts. *Sarcotheca monophylla* bears juicy red fruit and *Xerospermum noronhianum* bears fruit with a soft yellow seed coat. Next, their edible parts are rich in moisture (90.5% and 73.4%, respectively) and carbohydrate (54.8% and 76.7% on dry matter basis, respectively) as shown in Table V-11. Of course, because

Lariscus insignis has developed incisors but *Tupaia glis* does not, *Lariscus insignis* can utilize a wide range of fruits including some protected fruits with a hard seed coat (Table V-1). *Shorea maxima*, which bears acorn-like morphologically protected fruits, is a typical case. The two replications of the species showed high similarity ($C'_\lambda = 1.061$) and were classified into the cluster *Lariscus*. According to the photos, *Lariscus insignis* gnawed the fruit to eat the cotyledon, while *Tupaia glis* did not show such a behavior. *Tupaia glis* seems to eat portions of the fruit scattered on the ground by other species. There appears no competition between them in this case. This is why the similarity between the replications of *Shorea maxima* was high.

Plant species with low similarity between replications were favored by a wide range of animals (Tables V-3 & 4). The number of consumers of rattans and *Sarcotheca monophylla* were 12 and 9 species, respectively. Competition among consumers might be important in these cases.

(5) Availability of fruits

Two individuals of *Baccaurea parvifolia* ($C'_\lambda = 0.108$) were classified into the cluster *Macaca* subcluster *Macaca* and the cluster *Lariscus*, respectively (Table V-3, Fig. V-4). *Macaca nemestrina* was the dominant consumer in both experiments, as it accounted for 96.2% of the photos in the former, and 9.5% in the latter. The availability of fruit was different between the replications, as the former bore a much greater number of fruit than the latter. Therefore, it is thought that the latter tree was less important for *Macaca nemestrina* as a food resource.

Several replications of rattans showed low similarity. This might also result from differences in fruit availability. It is notable to point out that the similarity between the replications were not associated with the vegetation, but were caused by the lack of *Macaca nemestrina* (Table V-3). Therefore it is obvious that, in some cases, the

proportions of animal occurrence among replications are influenced by the availability of fruit.

In conclusion, the application of Morisita's similarity index to the data set obtained by the automatic camera system generally provides good results. The results are well independent of differences in several experimental conditions, such as period, location, and vegetation. Secondly, competition between consumers may have some influence on the results. Thirdly, the availability of fruit may affect the visiting frequency of consumers. It is necessary to use trees with an adequate amount of fruit for the study. In addition, the classifications using Morisita's similarity index and TWINSPAN were well coincident with each other (Table V-10), even though they are based on a different classification strategy. Therefore it can be concluded that the patterns of relationship between fruits and frugivores are well shown in this study.

Characters of porcupine-favored fruits

Several fruits were strongly preferred by *Trichys fasciculata* and were definitely classified into the cluster or group of *Trichys* (Figs. V-4 & 5, Tables V-3, 4, 5, 6, 7, & 8). They are *Knema hookeriana*, *Myristica cinnamomea* and *Myristica elliptica* (Myristicaceae), *Archidendron bubalium* and an unknown species of legume (Leguninosae), *Garcinia nervosa* (Guttiferae), *Dysoxylum acutangulum* (Meliaceae) and *Beilschmiedia madang* (Lauraceae) (Table V-12). These porcupine-favored fruits have two remarkable characters; (1) they are rich in protein or lipid and (2) have high energy content per unit weight (Table V-13).

Although the cotyledon of *Canarium littorale* and the seed of *Parkia speciosa* are rich in protein or lipid, they were not preferred by porcupines (Table V-13). There are two possible explanations for these exceptions; the quality and quantity of fruits. The cotyledon of *Canarium littorale* was mainly consumed by small rodents, namely *Leopoldamys sabanus* and *Lariscus insignis* (Table V-2). Because of the presence of a

hard and thick kernel and a small edible part, the cotyledon of *Canarium littorale* may be too poor in quality for *Trichys fasciculata*, while small rodents are probably more advantaged in handling the fruit. On the other hand, the seeds of *Parkia speciosa* were severely eaten by *Macaca nemestrina* and arboreal squirrels on the tree (Yasuda personal observations) and by *Macaca nemestrina* and *Sus scrofa* on the forest floor (Table V-2). These large mammals are common in the Pasoh forest (Lim *et al.* 1995) and usually move in groups (Medway 1978). Therefore, few seeds of *Parkia speciosa* remained on the forest floor. This may be the reason why *Trichys fasciculata* does not occur on the species, even though the seeds are rich in nutrient.

Community structure of terrestrial frugivores

The relationship between fruit characters and frugivores on the forest floor is shown in Fig. V-15. The frugivores are well scattered in the DCA plane. This might suggest the partitioning of fruit resources among frugivores. The first and the second axes are considered to represent the nutritional and the physical status of the fruit, as food resources for frugivores, because lipid, protein, and energy contents of fruits were negatively correlated with the first DCA axis (Fig. V-12 & 13) and the morphological protection of fruit was positively correlated with the second DCA axis (Fig. V-14).

Fruit size and color have been considered to be important factors in determining frugivore food preference of and to organize the frugivore community (Gautier-Hion *et al.* 1985). Gautier-Hion *et al.* (1985) suggested that there are two syndromes of fruit characters in an African tropical forest; bird-monkey syndrome and ruminant-rodent-elephant syndrome. The fruit characters of bird-monkey syndrome are brightly colored, have succulent pulp or arillate seeds, and no protective seed cover, while those of ruminant-rodent-elephant syndrome are large, dull-colored, and with a dry fibrous flesh, and well-protected seeds.

Many authors have argued that frugivores in tropical forests, especially primates, prefer colored fruits. Terborgh (1983) found that the only common feature of the fruits

consumed by primates in a Peruvian forest was a yellow to orange color. Julliot (1994) revealed that the fruits in either yellow, orange, or red accounted for 64.7% of the fruit consumption by Red Howler Monkeys in French Guiana. Sourd & Gautier-Hion (1986) found that forest guenon preferred brightly colored fruits and avoided dull-colored fruits in a Gabonese forest. In a Bornean forest, Leighton & Leighton (1983) found that primates frequently consume brightly colored fruits.

Such a tendency was not detected in the present study. *Macaca nemestrina*, one of the most terrestrial primates in Malaysian forests (Bernstein 1967; Medway 1978), preferred green fruits as well as colored fruits, as the species utilized 89.8% of surveyed fruits in the Pasoh forest (Table V-1). Another primate *Presbytis femoralis*, which is chiefly arboreal (Medway 1978), consumed both green and colored fruits, though the species occurred on only four species of plants (Table V-2). Leighton & Leighton (1983) concluded that Malaysian primates are fruit generalists, exploiting green flesh fruits as well as berries. Gould & Andau (1989) fed four species of Malaysian primates, including *Macaca nemestrina*, on some dull-colored fruits of dipterocarp under captive conditions, and found that some dipterocarp fruits are preferred by *Macaca nemestrina*. Stiles (1982) hypothesized that fruit color acts as "fruit flags" to display the fruits for the particular seed dispersers on the tree, but not for the secondary dispersers on the forest floor that act after the fruit fall. Therefore fruit color is thought to be less important in the present study for the terrestrial frugivores to determine fruit choice.

Animals that showed a preference for colored fruits were the water lizards (*Varanus* spp.) only, and for green fruits were *Hystrix brachyura* and *Tragulus javanicus*. The green fruits preferred by *Hystrix brachyura* were mainly species in the family Fagaceae (*Lithocarpus ewyckii*, *Lithocarpus lucidus*, and *Castanopsis megacarpa*), which bears thick-walled acorns or fruits with a spiny cupule. Those preferred by *Tragulus javanicus* contained *Canarium littorale* (Burseraceae) and *Terminalia citrina* (Combretaceae). They belong to different taxa, but both fruits are similar in morphology;

a hard kernel covered with leathery fibrous thick pulp, of which *Tragulus javanicus* utilized the pulp as food.

Although *Tupaia glis* is considered to be insectivorous, fruits comprise a considerable proportion of its food resources (Kawamichi & Kawamichi 1979; Langham 1982, 1983;). The present study revealed that *Tupaia glis* consumed 38.8% of the fruits surveyed (Table V-1), and preferred small, soft, and juicy fruits (Tables V-4 & 8), for instance, the juicy red fruit of *Sarcotheca monophylla* and the soft yellow seed coat of *Xerospermum noronhianum*, which are rich in moisture and carbohydrate (Table V-11). This is coincident with the finding of Emmons (1991) that *Tupaia glis* concentrates on small, soft, bird-dispersed fruits.

These facts on fruit preference of frugivores suggest that the patterns of fruit-frugivore relationship strongly depend on the digestive system of the animals. Rodents, including porcupines, have well-developed incisors as an adaptation to utilize morphologically protected fruits (Corbet & Hill 1992), while the mouse-deer has a forestomach enlarged into a rumen as a chamber for cellulose fermentation (Janis 1984). Treeshrews have undeveloped teeth, a small, simple stomach, a long, narrow small intestine, and narrow smooth large intestine (Emmons 1991).

Influence of frugivores on plants

As discussed above, the fruit morphology and nutrient contents are important factors in determining the food preference of frugivores, and the digestive system and foraging behavior of frugivores define the consequence of the fruit-frugivore interactions.

Macaca nemestrina is one of the most polyphagous fruit consumers in Malaysian forests. Fruits comprise about three quarters its food items (Caldecott 1986; Feeroz *et al.* 1994). Almost all the edible fruits in the Pasoh forest were consumed by the species (Table V-1). A variety of seeds were found in their feces (Yasuda personal observation). Due to its high population density and wide range of distribution in Malaysia (Medway

1978), *Macaca nemestrina* is considered to have a significant role in seed dispersal in Malaysian forests.

Some pulp consumers, such as *Tragulus javanicus*, *Lariscus insignis*, and *Tupaia glis*, may act as seed dispersers for some particular plants. They prefer morphologically unprotected fruits (Fig. V-15). Some of them are fruits with juicy pulp and tiny seeds and some are fruits with fleshy pulp and large seeds: for instance, *Sarcotheca monophylla* and *Canarium littorale*, respectively. Langham (1982) and Emmons (1991) suggest that *Tupaia* spp. are likely to act as seed dispersers of plants bearing small juicy fruits with tiny seeds. Furthermore, forest ruminants are considered to be important spit-type dispersers of fleshy fruits as well as endozoochory (through-the-gut) type dispersers (Feer 1995).

Moreover, animals having food hoarding behavior are effective dispersers (Howe & Westley 1988; Vander Wall 1990; Forget 1990, 1992, 1993, 1994, 1996). My colleague and I found food hoarding behavior in *Leopoldamys sabanus* and *Lariscus insignis* in the Pasoh forest (Yasuda *et al.* submitted). Since both of them are common terrestrial frugivores in the forest, as discussed previously, they might also act as seed dispersers after shedding fruits.

When the pattern and function of a fruit-frugivore interaction in a food web are revealed, the consequences of the interaction can be inferred. For example, porcupines prefer fruits with a high fat and energy content (Tables V-12 & 13). Since they gnaw to consume the cotyledons of such fruits exclusively, very few seeds can escape from predation (Miura *et al.* 1997). No information is so far available whether porcupines have hoarding behavior or not. If they do, they might be important seed dispersers. If not, they might be dominant seed predators for those particular plants, and I infer that such plants can recruit only in mast fruitings when predation satiation is achieved.

Chapter VI. Population dynamics and reproductive patterns of small mammals

Introduction

In this chapter, I discuss the population dynamics and reproductive patterns of some dominant terrestrial small mammals in the Pasoh Forest Reserve. The species concerned are *Leopoldamys sabanus*, *Tupaia glis*, and *Lariscus insignis*, all of which partially or considerably depend on fruits as food (Chapter V).

Some studies have been carried out on these ecological issues in aseasonal tropical forests of Southeast Asia. Malaysian forest rats have an annual reproductive cycle (Harrison 1955). Reproductive activity of *Tupaia glis* is concentrated in a particular period of the year (Wade 1958; Kawamichi & Kawamichi 1979; Langham 1982), and the breeding period of some fruit bats are coincident with fruiting seasons (Baker & Baker 1936; Lim 1970b). Medway (1972) inferred from his long term observation of plant phenology in a Malaysian forest that the reproductive seasonality in Malaysian forest rats reported by Harrison (1955) is probably associated with the plant reproductive phenology, because they depend on fallen fruits for food. However, this hypothesis has not been examined yet.

As discussed in Chapter III, the fruit production in Malaysian forests fluctuates largely from year to year. In Malaysia, the supra-annual cycles of plant phenology, known as mast fruiting, are more significant than the annual one. In order to grasp the gist of the population dynamics of frugivores, a long term study covering both normal and mast fruiting years is strongly required. However, most of the previous works were carried out over a short time and did not focus on the response of frugivore populations to mast fruiting.

Methods

Preparation of trapping data

In order to examine the population dynamics of small mammals, populations in PF were subjected to analysis, because phenological data is only available from PF for the whole period of the animal trapping (Chapter III).

Two data sets were extracted from trapping data using the following methods. The first is the sum of probabilities of individual occurrence in PF in a trapping session, which was used as "the number of captured individuals (*NI*)" in Chapter IV. A three month moving average was calculated for each species. The second was based on the monthly recapture records of individual animals in a trapping session, which represents another idea of the number of captured individuals. Even if an individual is recaptured more than once in PF, "the actual number of individuals (*NA*)" is considered as one. The minimum number of animals alive (*MNA*, LeDuc & Krebs 1975) represents the number of individuals captured in a trapping session (*NA*) plus those not captured in the session and recaptured again in subsequent months. *MNA* is advantageous in evening out the irregularities in capture of individuals and to examine the structure, fluctuation, and recruitment of a local population of which parameters are related to the reproduction, immigration, and emigration of individuals. A preliminary trapping period in February-May 1992 when bananas were used as baits and an additional trapping period in June 1996-January 1997 when oil-palm fruit were used as baits were taken into account as well as the main study period in June 1992-May 1996.

Definition of developmental stages

Developmental course of individuals after birth was divided into three stages: juvenile, subadult, and adult. The criteria of the thresholds between stages were as follows. Juveniles were distinguished by their appearance, principally by gray fur. Subadults were defined as immatures of which body weight did not exceed 80% of the mode of fully grown adults.

Results

Population fluctuation

(1) Correlation of density fluctuation at community level

In this section, the results based on *NI* are shown. At the community level, the density in total of small mammals decreased gradually during the main study period of animal trapping. Three-month moving averages of *NI* for the whole community (including the 13 spp. in Chapter IV), diurnal community (6 spp.) and nocturnal community (7 spp.) are shown in Fig. VI-1. The population density of the three dominant species are also shown. All of the three communities showed significant negative correlation with months of the study period ($p < 0.01$ for all the cases, df = 45). The correlation coefficients (r) were -0.728, -0.481, and -0.789, respectively.

Correlation coefficients of population fluctuation among the 13 species are shown in Table VI-1. The values underlined (eight out of 78 combinations of species) indicate significant positive or negative correlation with a particular species ($p < 0.05$, with Bonferroni adjustment). Among those significant combinations, seven were positive and the rest negative. There were no significant correlations among the most dominant species, *Leopoldamys sabanus*, *Tupaia glis*, and *Lariscus insignis*.

The density of small mammals increased when fruit availability in the habitat increased (Fig. VI-2). *NI* of the whole, diurnal, and nocturnal communities were fitted with parabolas against the index of fruiting (I_{fruit}) given in Chapter III. These coefficients of determination (r^2) were 0.463, 0.457, and 0.332, respectively (F-values = 18.6, 18.1, and 10.2, respectively, $p < 0.001$ for all cases, n = 46). The density of the three communities fluctuated at low levels when fruit availability was low, and rose steeply when fruit availability increased. The threshold between the two states was roughly 15 in the index of fruiting (Fig. VI-2).

(2) Correlation of population fluctuation at species level

The fluctuation of population densities of *Leopoldamys sabanus*, *Tupaia glis*, and *Lariscus insignis*, are shown in Fig. VI-3. Different sexes are shown separately. Except

for females of *Leopoldamys sabanus*, the populations of both sexes of the three species were at high levels at the beginning of the main study period and dropped rapidly within six to twelve months. Coefficients of variation (CV) of *Leopoldamys sabanus*, *Tupaia glis*, and *Lariscus insignis* were 28.7%, 40.3%, and 52.7% for females and 38.5%, 50.2%, and 57.0% for males, respectively. The population fluctuation of females of *Leopoldamys sabanus* was different from the others and more stable.

Population fluctuation among species and sexes were significantly correlated in several cases (Table VI-2). Females of *Leopoldamys sabanus* showed negative correlation with females of *Lariscus insignis* ($r = -0.521$, $p < 0.003$ with Bonferroni adjustment, df = 45). Males of *Leopoldamys sabanus* showed positive correlation with females of *Tupaia glis* ($r = 0.558$, $p < 0.001$ with Bonferroni adjustment, df = 45). *Tupaia glis* and *Lariscus insignis* showed positive correlation between different sexes of the same species ($r = 0.562$, $p = 0.001$ for *Tupaia glis*; and $r = 0.428$, $p = 0.045$ for *Lariscus insignis*; df = 45, Bonferroni adjustment). The combination between females of *Tupaia glis* and males of *Lariscus insignis* also showed positive correlation ($r = 0.442$, $p = 0.032$ with Bonferroni adjustment, df = 45).

(3) Fruit availability and population fluctuation

The lag correlation between fruit availability and the population fluctuation of the three species are shown in Figs. VI-4, 5, & 6. Populations of males of *Leopoldamys sabanus*, females of *Lariscus insignis*, and females of *Tupaia glis* showed significant positive correlation with fruit availability without time lags (lag = 0) for the former two ($r = 0.504$ and 0.492, respectively, $p < 0.05$) and with a one month lag (lag = -1) for the latter ($r = 0.575$, $p < 0.05$), respectively. The latter case indicates that population increase precedes the rise in availability of fruits by one month.

Populations of the three species were plotted against fruit availability and fitted with parabolas (Fig. VI-7). Coefficients of determination (r^2) were 0.061, 0.314, 0.155, 0.569, 0.321, and 0.356 in the order of females and males of *Leopoldamys sabanus*,

Tupaia glis, and *Lariscus insignis* (F-values were 1.51, 9.20, 3.85, 24.3, 10.4, and 10.1, respectively; df = 2). All cases, except for females of *Leopoldamys sabanus*, showed significantly good fit (p < 0.05).

Development of juveniles

Frequency distributions of body weight are shown for the three species (Fig. VI-8), based on the four-year data of the main trapping period. When the proportion of juveniles in a weight class was 50% or more, the weight class was considered to be in the juvenile stage. The thresholds between juvenile and subadult were given as 220, 100, and 130 g in body weight for *Leopoldamys sabanus*, *Tupaia glis*, and *Lariscus insignis*, respectively. Those between subadult and adult were set as 300, 120, and 160 g, respectively (Fig. VI-8).

Six individuals of *Leopoldamys sabanus* (two females and four males) were recaptured frequently in the early stage of their development. Two of them (one female and one male) kept staying in the study plot for more than 20 months and showed the complete course of body development of the species from juvenile to fully grown adult under natural conditions. Since the age of an individual at initial capture was unidentified, I assumed that the weight classes of 70-100 and 130-170 g are one month and two months old, respectively (after Harrison 1956; Rudd 1965), the body growth of *Leopoldamys sabanus* was fitted by a logistic curve to the pooled data of the six individuals (Fig. VI-9). The regression equation was given as:

$$W = 71.49e^{0.528t}/\{1 + 71.49(e^{0.528t} - 1)/355.66\},$$

where W is body weight in grams and t is age in months. Using this regression equation, the thresholds between juvenile and subadult ($W = 220$ g) and between subadult and adult ($W = 300$ g) of *Leopoldamys sabanus* were estimated as about 3.5 and 6.0 months old, respectively.

For the other two species, *Tupaia glis* and *Lariscus insignis*, the number of recaptures was not sufficient to derive regression equations.

Population dynamics and reproduction

(1) Ratio of exposed individuals by trapping

In the sections below, the results based on *NA* and *MNA* are shown. Figure VI-10 shows the ratios of individuals exposed by trapping in a trapping session, which is given by the ratio of *NA* to *MNA* of the month. The details of *NA* and *MNA* for each sex of the three species will be shown later (Figs. VI-11, 12, 17, 18, 20, & 21). The ratios of *Leopoldamys sabanus* were steady at high levels for both sexes (mean = 84.3% for females and 72.0% for males, n = 48), except for the population of males in March 1995 when no individual was captured. The ratios of *Tupaia glis* were lower than those of *Leopoldamys sabanus* (mean = 47.3% for females and 36.5% for males, n = 48). Those of *Lariscus insignis* largely fluctuated between 0-100%, due to the small number of *NA* and *MNA*. The ratios of the species on average were 67.1% and 48.0% for females and males, respectively.

(2) A case study: *Leopoldamys sabanus*

Population dynamics

Changes of *NA*, *MNA*, and newly captured individuals of *Leopoldamys sabanus* are shown in Figs. VI-11b & 12b for females and males, respectively. Newly captured individuals are divided into two categories: juveniles and new adults. The latter category consisted of the stages of subadult and adult by body weight. The survival of pseudo-cohorts are shown in Figs. VI-11c and 12c for females and males, respectively. I use the term "pseudo-cohort" to refer to populations that consist of individuals for which initial captures were made at the same trapping session, irrespective of their age. The period shown in these figures was from February 1992 to January 1997, including the mast fruiting event in 1996.

The population density of females of *Leopoldamys sabanus* was lower and more stable than that of males (Figs. VI-11-b and 12-b). The averages of *MNA* were 4.96 ± 1.49 SD and 7.35 ± 2.61 SD individuals for females and males, respectively, and the coefficients of variation (CV) were 30.0% and 35.4%, respectively (calculation based on the data from June 1992 to May 1996 because of the low trap success rates during the mast fruiting event; see Fig. IV-1).

The number of wandering individuals, which was represented as the differences between *MNA* and *NA*, was larger in males (1.85 ± 0.18 SE ind.) than in females (0.73 ± 0.11 SE ind.). The ratio of wandering individuals to *MNA* were significantly different between sexes, as 28.0% for males and 15.9% for females on average (p = 0.003, Sign-test, two-tails, n = 48).

Synchronous disappearance of individuals

There were several drops in survival of pseudo-cohorts for both sexes (Fig. VI-11c & 12c), which represent the synchronous disappearance of individuals. To see the details, the emergence and disappearance of individuals are shown in Fig. VI-13. Disappearance was divided into two categories according to length of stay in the study plot. One was "short stay" which refers to individuals for which length of stay was only one month, in other words, these individuals were not recaptured in the months following initial captures. A second was "long stay" which refers to individuals for which length of stay was two or more months before disappearance.

Synchronous disappearance, which is defined as three or more "long stay" individuals disappearing in consecutive months, occurred in October-December 1992, June-August 1993, July-August 1994, February 1995, and February-April 1996 in females, and September-November 1992, January-March 1993, September-October 1993, December 1993-February 1994, July-October 1994, January-February 1995, and December 1995-March 1996 for males. The periods of synchronous disappearance

seemed to be coincident between sexes and tended to correspond with drops in fruit availability in the habitat (Fig. VI-11 & 12).

Estimation of month of birth

Seven female and nine male juveniles were captured in PF during the whole study period. Juveniles emerged in clusters in middle-late 1992, 1994, and 1996, while new adults were captured continuously during the study period for both sexes (Figs. VI-11b & 12 b). Using the regression equation of age-body weight relationship (Fig. VI-9), the months of birth of juveniles and subadults were estimated (Fig. VI-14). The months of birth were well coincident with the periods of higher productivity of fruits ($p < 0.0001$, Pearson's phi correlation coefficient = 0.88, $\chi^2 = 30.2$ with Yates' adjustment, n = 45). The threshold between good fruiting and bad fruiting periods used here was 10.0 in the three-month moving average of the index of fruiting (Fig. VI-14a).

Reproductive condition of individuals

Figures VI-15 and 16 show the reproductive conditions of females and males in *Leopoldamys sabanus*. Three-month moving averages of *NA* are presented. Reproductive females consisted of the categories pregnant and lactating, and for reproductive males consisted of the categories active and very active. There were some reproductive individuals in PF throughout the study period, though their numbers and proportions fluctuated greatly in time (Figs. VI-15 & 16).

The proportion of reproductive females was at a high level ($\geq 50\%$) at the beginning of the study period, when fruit productivity was high. The proportion decreased gradually and remained at a low level in 1993 with some variation. Then, the proportion suddenly increased from 35.7% in March to 64.3% in April 1994, when the fruit productivity of the habitat started to rise. The higher reproductive period of females remained until August 1995, then dropped suddenly and reached its lowest (0.0%) in November 1995. After that, the proportion of reproductive females recovered again

toward the end of the study period. It is notable to point out that the dip in mid 1996 was due to the low trap success rate in the mast fruiting event.

The proportion of reproductive males was steady at a high level ($\geq$ 80%) during the study period with some exceptions (Fig. VI-16). There were four drops in the proportion; their lowest points were in February 1993, August 1994, February-March 1996, and December 1996. These drops were caused by the recruitment of individuals that were sexually immature, and not by seasonal change in reproductive conditions of adult individuals. Figure VI-17 shows the reproductive conditions of individuals that stayed six months or more in PF. Males remained sexually active for a long time without changing their reproductive condition between inactive (-, +) and active (X), while some females changed their reproductive condition between normal (-) and pregnancy or lactating (X) in time.

(3) Comparative studies: *Tupaia glis* and *Lariscus insignis*

Population dynamics and reproduction of *Tupaia glis*

Changes in *NA*, *MNA*, and newly captured individuals of *Tupaia glis* are shown in Figs. VI-18 and 19 for females and males, respectively. *MNA* of both sexes were quite stable. Mean *MNA* for four years from June 1992-May 1996 were 6.15 $\pm$ 1.60 SD and 4.56 $\pm$ 1.29 SD individuals for females and males, respectively. Longevity of pseudo-cohorts was quite long, and sometimes more than 30 months in both sexes. Some individuals were recaptured after a long absence.

Since very few juveniles of *Tupaia glis* emerged in PF, all juveniles captured over the whole 10 ha plot were subjected to analysis. Sixteen juveniles were captured in total; in July-August 1992, April and August 1993, May-June and December 1994, March and July-August 1995, June 1996, and November 1996-January 1997 (Figs. VI-18b & 19b). According to the growth rate of *Tupaia glis* given by previous studies (Morris *et al.* 1967; Shimada 1973), months of birth were estimated assuming that the age of juveniles ($W <$ 100g) and subadults ($100 \leq W < 120$ g) are one month old and two months old,

respectively (Fig. VI-20). There was no significant correlation between fruit production ($I_{fruit} \geq 10.0$) and breeding seasons of *Tupaia glis* (Pearson's phi correlation coefficient = 0.111, p > 0.5, n = 54). When the month of birth for all juveniles was lumped together in a calendar month, there were two modes in May-July and October-December. The former occurred in normal years, while the latter occurred in late 1996 just after the mast fruiting event.

Further analysis could not be executed for *Tupaia glis*, because of the small number of *NA* and *MNA* of the species.

Population dynamics and reproduction of *Lariscus insignis*

Population dynamics of females and males of *Lariscus insignis* are shown in Figs. VI-21 & 22. *MNA* of both sexes were highest at the beginning of the study period, as 8 and 12 individuals for females and males, respectively. After the population densities had dropped, *MNA* remained low (2-3 individuals) in females, and recovered to 5-7 individuals in males. Mean *MNA* for four years from June 1992-May 1996 were 3.13 ± 2.14 SD and 5.05 ± 2.45 SD individuals for females and males, respectively. Longevity of pseudo-cohort sometimes exceeded 12 months, with a maximum of 25 months.

In total, ten individual juveniles emerged in the 10 ha study plot through the study period, and the month of birth of each individuals was estimated assuming that the ages of juveniles ($W < 130$ g) and subadults ($130 \leq W < 160$ g) were 1 month old and 2 months old, respectively (Fig. VI-23). Statistically, there was no significant correlation between fruit production ($I_{fruit} \geq 10.0$) and breeding seasons of *Lariscus insignis* (Pearson's phi correlation coefficient = 0.157, p > 0.5, n = 54). However, breeding seasons derived from the estimated month of birth seemed slightly clustered (Fig. VI-23).

Further analysis of the reproduction of *Lariscus insignis* could not be undertaken, because of the low population density of the species.

Discussion

Breeding season of *Leopoldamys sabanus*

Based on five year removal trapping in a tropical rain forest in Selangor in Peninsular Malaysia, Harrison (1955) found that pregnant females of *Leopoldamys sabanus* existed through the year but more occurred in July-September, and that the proportion of fertile (sexually active) males was higher in April-September than in October-March. The same tendency was also found in the same study in another rat, *Sundamys muelleri*, (Harrison 1955). He could not give any plausible reasons for the reproductive seasonality of these species, since he had little information of the environmental factors that could influence their reproduction and population dynamics. As fruiting in the region was concentrated in July-December, Medway (1972) inferred that the seasonal breeding of forest rats reported by Harrison (1955) might be associated with the fluctuation of food availability in the forest, especially the seasonality of fruit production.

Leopoldamys sabanus feeds extensively on fruits on the forest floor, as well as animal materials (Harrison 1954, 1961; Lim 1970a). Lim (1970a) found that fruits accounted for 36.5% of the stomach contents of the species by frequency. As discussed in Chapter V, I showed that *Leopoldamys sabanus* utilizes a wide spectrum of fruits.

The present study revealed that the proportion of reproductive females of *Leopoldamys sabanus* fluctuated greatly in time and that the breeding seasons were coincident with the fruiting seasons of good fruiting years (Figs. VI-14 & 15). According to Harrison (1955), the females of *Leopoldamys sabanus* are considered to be potentially fertile when body weight is greater than 220 g, which represents age of about 3.5 months (Fig. VI-9). During the poor fruiting seasons from late 1993 to early 1994, the proportion of reproductive females was low ($\leq$ 30% of individuals, Fig. VI-15), though all the females were mature enough in body size ($W = 285$-370 g, n = 26). In the following year, there was an immediate sharp increase in the proportion of reproductive females in April, which was coincident with the onset of the fruiting season of that year. The number of reproductive females reached a peak in June 1994 (Fig. VI-15b) and this breeding

season continued until mid 1995 (Fig. VI-15c). A similar fluctuation occurred from late 1995 to the end of 1996 when the mast fruiting occurred. Note that the drop in the proportion of reproductive females in mid 1996 (Fig. VI-15c) may be apparent due to a low trap success rate in the mast fruiting event. Moreover, juveniles emerged in clusters in good fruiting periods (Fig. VI-14). These results generally agree with Harrison's (1955) finding that pregnant females of *Leopoldamys sabanus* are more common in July-September, but do not agree with his conclusion that *Leopoldamys sabanus* has an annual reproductive cycle related to the calendar month. The present study strongly suggests that the reproduction of *Leopoldamys sabanus* is supra-annual and dependent on the fruit availability in the habitat. Mull & Lim (1974) also suggested supra-annual reproductive cycles of flying squirrels in Malaysian forests. The females may decide to breed depending on the food supply in their own home ranges, and the threshold to switch to breeding might be about 10.0 in fruiting index (Fig. VI-14). This reproductive behavior is quite adaptive because pregnancy and lactation require sufficient surpluses of nutrients and energy for females.

In total, eight individuals of *Leopoldamys sabanus* were estimated to be born in March-November 1994 in a cluster (Fig. VI-14). Their estimated months of birth were well coincident with the fruiting season of the year. Here, a problem arises on the timing of breeding. Although so far no information is available on the gestation period of *Leopoldamys sabanus*, it may be close to one month, because the gestation periods of three quarter of Rodentia (112 spp. were investigated) are less than 40 days and those of muridae range from 18-38 days (Frazer & Huggett 1974; Millar 1981). Species with longer gestation periods (> 40 days) are larger rodents, such as porcupines, beavers and agoutis. Therefore, the estrus of *Leopoldamys sabanus* should precede the onset of fruiting season by at least one month in order to match the time when they nurse their young with the peak availability of fruits.

A similar phenomenon is seen in birds. A number of bird species regulate their breeding seasons to match the peak availability of food with the time when they have

young in the nest (Lack 1954; Perrins & Birkhead 1983). In blue and great tits, which feed their young on caterpillars, the period when young tits are in the nest coincides in general with the time of abundance of caterpillars, and the annual variations in the breeding seasons of the tits are paralleled by the appearance of caterpillars (Gibb 1950). It is said that air temperature is a possible proximate factor to determine the timing of breeding in the tits (Perrins 1979, 1991; van Noordwijk *et al.* 1995).

The proximate factors in determining the timing of breeding in *Leopoldamys sabanus* are not known. Since a good fruiting season is usually preceded by a good flowering season (Fig. III-8) and *Leopoldamys sabanus* is a good climber (Lim 1970a), it might be possible for females of *Leopoldamys sabanus* to estimate food abundance in their own home ranges in the near future.

Lastly, the synchronous disappearance of female individuals (Fig. VI-13a) may be associated with the reproductive activity of these individuals. Figure VI-17 shows that the disappearance of long stay females usually occurred after reproduction. I surmise that this may be due to the exhaustion of females by reproduction and nursing.

Reproductive strategy in males of *Leopoldamys sabanus*

Another argument in Harrison (1955) is that there are annual cycles in testis weight of fertile males and in proportion of non-fertile males of *Leopoldamys sabanus*. Such tendencies were not found in the present study. The proportion of reproductive males was relatively steady at a high level (Fig. VI-16c), even during the low reproductive periods in females (Fig. VI-15c). Resident adult males kept their fertility for a long time until their disappearance and showed no obvious reproductive cycles at the individual level (Fig. VI-17b). The periodical drops in the proportion of reproductive males in Fig VI-16c were due to the recruitment of immature individuals to the local population. I suggest that Harrison's (1955) finding on the reproductive cycles of males may be an apparent phenomenon that was caused by his study method, i.e. removal trapping, which did not allow him to follow individual reproductive conditions. Mull &

Lim (1974) advised that reproductive data over a period of years should not be lumped together in a calendar month.

The proportion of wanderers was higher in males than in females (Figs. VI-11b & 12b). A considerable portion of wanderers were fertile as well as residents. This implies that there are two types of strategy in males: residents and wanderers. Residents settle their home ranges and copulate with neighbor females, while wanderers do not settle their home ranges and wander to look for females in estrus. As discussed in the previous section, females of *Leopoldamys sabanus* seem to decide their reproductive condition depending on the fruit availability. This may be the reason why the population density of males of *Leopoldamys sabanus* shows a positive correlation with fruit availability without lags (VI-4b), while that of females does not show such a tendency (Fig. VI-4a). Therefore, the synchronous disappearance of individuals in males (Fig. VI-13b) might be associated with the emigration of wanderers from the center of reproduction.

In conclusion, the fruit availability in the habitat determine the reproductive condition of females directly and the migration of males indirectly. This suggests that bottom-up processes are significant in the population regulation of *Leopoldamys sabanus*.

Breading season of *Tupaia glis* and *Lariscus insignis*

Tupaia glis mostly feeds on insects, although the species readily eats fruits (Harrison 1961; Vandenberh 1963; Kawamichi & Kawamichi 1979; Langham 1983; Emmons 1991). According to Langham (1983), fruits accounted for 25.0% of the stomach contents of *Tupaia glis* by frequency. My observations using the automatic camera system revealed that *Tupaia glis* prefers soft and juicy fruits (in Chapter V).

Based on removal trapping in Selangor in Peninsular Malaysia, Lim (in press) found that more pregnant females of *Tupaia glis* were captured in March-June. In the present study, more than half (9 out of 17 cases) of juveniles of *Tupaia glis* ($W < 100$ g) were captured in June-August and were estimated to be born in May-July (Fig. VI-20b).

Since the gestation period of *Tupaia glis* is 46-50 days (Hendrickson 1954), females should be in estrus in March-June. This result is well coincident with that of Lim (in press) and the breeding season of this species is well coincident with that of *Leopoldamys sabanus*. It is notable to point out that the breeding season of the species seems more periodical in comparison with that of *Leopoldamys sabanus* (Fig. VI-20).

Lariscus insignis also prefers soft and juicy fruits on the forest floor (Chapter V). Birth of new individuals scattered over calendar months and no seasonality in breeding were recognized (Fig. VI-23). This may be due to the small number of juveniles and subadults captured during the study period.

Population densities of females of *Tupaia glis* and females of *Lariscus insignis* were positively correlated with fruit availability in the forest, while those of males in both species did not show such a tendency (Figs. VI-5 & 6). However, there were significant positive correlations of population fluctuation between sexes in both species (Table VI-2). The pair type or harem type social structure of *Tupaia glis* (Kawamichi & Kawamichi 1979, 1982) may lead to positive correlation of population fluctuation between sexes.

Breeding season of small mammals in Southeast Asia

The breeding season of small mammals tends to synchronize among species in a given area but differ locally. The peak breeding activity of small mammals reported in previous works were, from north to south, in March-May in central west Thailand (Walker & Rabinowitz 1992), February-June in Penang and Kedah, Malaysia (Langham 1982), March-June in Selangor, Malaysia (Lim in press), May-July in Negri Sembilan, Malaysia (the present study), and December-March in Singapore (Kawamichi & Kawamichi 1982). In addition, breeding activity in north Borneo occurs in June-August (Wade 1958). These studies, which were conducted on the small mammal communities dominated by *Leopoldamys sabanus* and/or *Tupaia glis*, suggest that the breeding season of these small mammals has a latitudinal gradient over the region from Thailand to Peninsular Malaysia, since the northern populations breed earlier than the southern ones.

The breeding season seems to more or less coincide with the onset of the rainy season at the location (Dale 1959), except in the case of north Borneo, where the breeding season is in the middle of the lower precipitation period (Wade 1958).

However, precipitation is not an important factor in determining plant phenology in aseasonal tropical rain forests in Southeast Asia (Ashton *et al.* 1988). Corlett (1990) found that the typical fruiting season in Singapore is in June-August, though the intensity of fruit production varies from year to year. The breeding period of *Tupaia glis* in Singapore as reported by Kawamichi & Kawamichi (1982) was December-March, which does not seem to be related to the fruiting season in the region. Their study was conducted from October to the following March, so that they might have no chance to observe the actual breeding season of *Tupaia glis* in Singapore. Kawamichi & Kawamichi (1979) mentioned that a large fig tree in their study site supplied a large quantity of fig fruits in February-March in their observation period, and found that not only the tree owners but also non-residents and residents that occupied territories in adjacent areas came to eat the fig fruits frequently. Then, one of the visitors showed estrus as well as the tree owner. This implies that the reproduction of *Tupaia glis* is influenced not only by calendar months but also by local fruit availability. I suggest that small mammals can respond to breed due to the sporadic fruiting of individual trees during a non-fruiting season. Such a food supply is quite patchy; consequently, the food availability for an individual is improved considerably when the individual occupies the patch. This tendency might spread widely among frugivrous small mammals that inhabit the aseasonal tropical forests of Southeast Asia.

Impacts of mast fruiting on a small mammal community

Some small mammals in the Pasoh forest breed in the fruiting seasons of normal years as well as in the mast fruiting event. Food supply is a significant factor in determining their population regulation (Chapter VI). The significance of bottom-up processes in population regulation of small mammals was also found by many previous

studies in tropical forests (Adler & Beatty 1997) as well as in temperate forests (Taitt & Krebs 1981; Ims 1987; Hubbs & Boonstra 1997).

The total density of small mammals was higher at the beginning of the present study and gradually decreased in time until the onset of the mast fruiting (Fig. VI-1). The higher animal density in 1992 might have been caused by the previous mast fruiting in 1989 reported by LaFrankie & Chan (1991). The trend of population decline through the non-mast fruiting years implies that the local population of small mammals can not fully compensate for the loss of individuals by mortality and emigration in normal years. More juveniles and subadults were estimated to be born in the mast fruiting of 1996 (Figs. VI-14 & 20), though they should be underestimated due to the low trapping success in the period. Therefore fully compensatory population recruitment would be achieved in mast fruiting events when plentiful food in the habitat promotes the reproduction of small mammals.

Chapter VII. General discussion

This thesis dealt with the functional aspects of plant-frugivore interactions in a Malaysian tropical rain forest community. It revealed that nutrient contents and morphological protection of fruit determine the relationships between fruits and frugivores and that plants influence animal populations through their reproductive activity. I suggested that animals influence plant populations through their foraging behavior, i.e. fruit consumption and hoarding behavior. There is a circular interaction between them, and it is considered to be essential to maintain the ecosystem. This thesis provides valuable information for the understanding of the complex community, especially on the structure and function.

Evolutionary factors of mast fruiting

The low food productivity in the intervals of mast fruiting events keeps the density of seed predators at low levels (Chapter VI). As a consequence, predation satiation (Janzen 1974) may be achieved by the overwhelming fruit crops in a mast fruiting event. However, this is merely a consequence of masting, not the proof of the hypothesis that predation satiation is a major factor driving the evolution of the phenomenon.

I do not agree with the predation satiation hypothesis as a major evolutionary factor for mast fruiting in the tropical rain forests of Southeast Asia, though I think that predation satiation can reinforce the masting behavior after it has been established (Yasuda 1997).

During mass flowering, individuals of certain plant species are known to flower in tight synchrony, whereas groups of closely related species appear to exhibit slightly discordant phenologies, known as "sequential flowering" (Chan & Appanah 1980; LaFrankie & Chan 1991). After a few months from flowering, fruit shedding occurs within a short period in synchrony among individuals and species (Chan 1980). The timing of fruit shedding is coincident with the onset of rainy season, suggesting that

synchronous fruiting is an adaptation to match germination with the more suitable period for seedling establishment (germination hypothesis, Burgess 1970). The predation satiation hypothesis does not identify the timing of fruit shedding, while the germination hypothesis does. Therefore the germination hypothesis is more plausible in explaining why fruits are shed gregariously in a season. On the other hand, the sequential flowering is an elaborate phenomenon in which the same pollinators are shared among closely related species of plants, suggesting that the evolution of mast fruiting is considered to be associated with plant-pollinator interactions in the mass flowering (Inoue 1997). The phylogenetic constraints of a phenological cue for mass flowering may be also important complementarily (Ashton *et al.* 1988).

Are there any keystone species in the community?

Ficus spp. have been considered to be typical keystone species in tropical rain forests (Terborgh 1986; Leighton & Leighton 1983; Lambert & Marshall 1991; Poonswad & Kemp 1993) because fig trees bear fruits throughout the year (Corlett 1987; Foster 1996) and frugivores depend on fig fruits as food during food scarcity (Whitmore 1990). The relationship between figs and their consumers is thought to be a case of coevolution (Whitmore 1990). Typical cases in Southeast Asia were reported from a Bornean forest (Leighton & Leighton 1983) and a Malayan forest (Lambert & Marshall 1991).

However, *Ficus* spp. are not considered to be in the same ecological status in the Pasoh forest. First, species diversity and population densities of figs in the Pasoh forest are lower than other rain forests of Southeast Asia. Ten species of *Ficus* were recorded in the Pasoh 50 ha plot (Manokaran *et al.* 1992), which accounts for only 9.9% of all the known species of the genus in Peninsular Malaysia (Kochumen 1978), while 27 species in 74 ha at Kuala Lompat, Peninsular Malaysia (Lambert & Marshall 1991) and 75 species and varieties at the Lambir National Park, Sarawak (Harrison 1997; the size of the study area is not described) were recorded. Although the lower species diversity of figs in

the Pasoh forest may be partially due to excluding epiphytic figs from the census, the population densities of non-epiphytic figs in the forest are quite low, in the range of 0.04-0.96 ind./ha. The total density of large fig trees (dbh $\geq$ 5 cm) was 0.24 ind./ha in Pasoh (Manokaran *et al.* 1992), while that was 4.95 ind./ha in Kuala Lompat (Lambert & Marshall 1991). Secondary, I scarcely found fruiting fig trees and epiphytes during the study period. Figs in my study area bore fruits discontinuously, not only at the individual level but also at the community level. Thirdly, several individuals of *Ficus* spp. were used for the automatic camera experiments and only a small number of photos were taken. These suggest that figs are too minor to be keystone resources for frugivores in the Pasoh forest. This may be a characteristic of the Pasoh Forest Reserve, which is located in the driest part of the Malay peninsula (Dale 1959). Gautier-Hion & Michaloud (1989) also found that figs were not the keystone species in an African forest.

There were some fruiting species in non-fruiting seasons in normal years, but the density of fruiting trees was sometimes extremely low (Chapter III). Previous studies suggest that fig fruits are supplemented by the fruits of climbers of the family Annonaceae and by some Meliaceae and Myristicaceae (Whitmore 1990). However, as discussed in Chapter V, no alternative plants were identified as the keystone resources for frugivores in the Pasoh forest, because the fruiting species in non-fruiting seasons belonged to a variety of taxa and most of them did not bear fruits repeatedly. I suppose that the concept of "keystone species" is too useful to stress the importance of the interactions including the species, however, the concept is not applicable to some tropical rain forest communities.

Effects of logging on a mammalian community

Forest fragmentation and isolation are considered to be the major factors threatening the mammalian fauna in Malaysia (Bennett 1991; Zaaba *et al.* 1991). Harrison (1968) studied the effects of forest clearance on Malaysian mammals in lowland rain forests, and found that the number of species decreased markedly from primary forest

through secondary forest to scrub and grassland. He suggested that the depletion of mammalian fauna results from the loss of large mammals.

Fruit is a resource patchily scattered in a forest. The long period of less fruiting between mast-fruiting events in the study region may cause a higher probability of food shortage for frugivores, and especially in fragmented and diminished forests, fruit supply may not be enough to support the populations of frugivores any longer. Considering that the Pasoh Forest Reserve covers only 2,500 ha of almost isolated forest and about a half of it consists of less productive habitat of secondary vegetation, the limitation of food supply could be the reason why large frugivores seen in the Pasoh forest in the past have not been reputed recently (Kemper 1988; Lim *et al.* 1995), for instance, the Asian elephant (*Elephas maximus*), Tapir (*Tapirus indicus*), Sambar deer (*Cervus unicolor*), and some frugivorous primates (e.g. *Hylobates* spp.).

The situation seems different for small mammals. Most of the Malaysian small mammals prefer primary forest habitat (Stevens 1968; Harrison 1969; Lim 1970a; Zubaid & Rizal 1995; Zubaid & M. Khairul 1997; Chapter VI in the present study), however, Harrison (1968) suggested that selective logging of primary forest does not seriously deplete the number of species of small mammals. The present study agrees with this partially. The diversity of small mammals in number of guilds was steady during the study period (Fig. IV-6b), even though there were some periods of fruit scarcity. Their populations are considered to be relatively tolerant toward severe environmental stresses, because most of the small mammals are omnivorous-frugivores (Harrison 1954, 1961; Lim 1966, 1970a; Medway 1978; Langham 1982, 1983; Payne *et al.* 1985; Emmons 1991), have smaller home ranges (Harrison 1958; Sanderson & Sanderson 1964; Lim & Zubaid 1995), high population densities (Lim 1970a; Langham 1983; Walker & Rabinowitz 1992; Zubaid & Rizal 1997), and high reproductive rates (present study), and may require less energy to maintain themselves because of their small body size.

There was a large difference between a primary forest and an old secondary forest in relative species composition, though the number of species captured was similar

between them (Chapter IV). It is obvious that the small mammal community in the secondary forest is still under the influence of logging carried out in the 1950s, even though it has been untouched for about a half century after the logging and small mammals have high reproductive capacity and mobility in general. The present study suggests that logged forest needs a quite long time to recover from logging disturbance to provide sufficient environmental conditions for small mammals (Chapter III & IV).

Concluding remarks: the application for the tropical rain forest conservation

This thesis also provides information for the conservation of tropical rain forests. I emphasis that any management plans for tropical rain forests should consider their animal inhabitants as well. Frugivores may utilize little of the system's energy but are essential parts of the ecosystem as seed dispersers. The loss of dispersal agents could cause a cascading decline of biodiversity of the forest in the near future.

Logging and forest fragmentation have a strong influence on the frugivore community over several decades. Squirrels are most vulnerable to logging disturbance in the small mammal community (Chapter IV) and are considered to be important seed dispersers (Ridley 1894; Becker *et al.* 1985). *Macaca nemestrina*, which is vulnerable to forest fragmentation (Bennett 1991), is a generalist in fruit consumption and thus it may act as an important seed disperser for a variety of plant species (Chapter VI).

The present study revealed certain important factors to maintain viable populations of frugivores. In order to regain and maintain the vitality of the forest in general, the most necessary and realistic steps are the artificial treatments of degraded forests to promote better habitats for common and unthreatened frugivores, for example, the construction of corridors to promote animal movement among isolated forests, enrichment of the forest with indigenous fruit-bearing trees, and artificial thinning for the better development of forest.