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FORAGING ACTIVITY PATTERNS OF FRUGIVOROUS OR OMNIVOROUS ANIMALS ON THE FOREST FLOOR OF A TROPICAL SEASONAL FOREST IN THAILAND, WITH REFERENCE TO SEASONAL CHANGES

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ABSTRACT

The present study quantitatively described the diel foraging activity patterns of frugivorous or omnivorous animals on the forest floor of a tropical seasonal forest in Thailand and showed the seasonal changes in the activity patterns of some species. The activity patterns were investigated using automatic camera systems baited with fruits on the forest floor. A total of 11,133 pictures were taken. Forty-eight animal species could be identified in 10,955 pictures, including 30 species of mammals, 17 birds and 1 reptile. Analyses were made for the diel activity patterns of animals for which 30 or more visits had been recorded. Based on the temporal distribution of visits, 18 analyzed species were classified into the following three categories: (1) diurnal species, not active at night, (2) nocturnal species, not active during the day, (3) others, active during both day and night. The results of the classification were as follows: 2 mammals (*Macaca nemestrina, Callosciurus finlaysonii*) and 3 birds (*Chalcophaps indica, Pitta cyanea, Garrulax leucolophus*) were diurnal with an almost unimodal temporal distribution; 2 mammals (*Tupaia belangeri, Menetes berdmorei*) and 3 birds (*Lophura diardi, Gallus gallus, Arborophila chloropus*) were diurnal with a bimodal temporal distribution; 5 mammals (*Rattus* spp., *Niviventer fulvescens, Leopoldamys sabanus, Maxomys surifer, Hystrix brachyura*) were nocturnal; 3 mammals (*Tragulus javanicus, Cervus unicolor, Muntiacus muntjak*) were the others. There were significant differences in the temporal distribution of visits between the rainy and dry seasons for the Malayan porcupine (*Hystrix brachyura*), Siamese fireback (*Lophura diardi*) and red jungle fowl (*Gallus gallus*).

Key words: activity pattern, camera trapping, crepuscular, diurnal, feeding activity, Khao Yai National Park, nocturnal

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INTRODUCTION

Tropical forests provide enormously diverse and complex habitats and harbor many mammal and bird species (HARRISON, 1962; MIURA *ET AL.*, 1997; YASUDA *ET AL.*, 2005). WHITMORE (1990) presented a schematic figure describing the space and time partitioning of mammals in a tropical rain forest in Borneo, by which coexistence may be facilitated. However, quantitative studies on activity patterns, which are an essential component for understanding time partitioning, have been relatively insufficient for animals of tropical forests (VAN SCHAIK & GRIFFITHS, 1996; MIURA *ET AL.*, 1997; KAWANISHI & SUNQUIST, 2004).

Several studies conducted in temperate zones have shown that activity patterns of mammals change seasonally in accordance with environmental factors such as air temperature, day length, and precipitation (PEARSON, 1960; OSTERBERG, 1962; TANAKA, 2005). Although tropical seasonal forests also experience marked seasonal changes in precipitation, nothing is known about seasonal changes in the activity patterns of animals living in tropical seasonal forests.

In recent years, automatic camera systems have been utilized in ecological research on animals (PEARSON, 1960; CARLEY *ET AL.*, 1970; GREENWOOD, 1978; GRIFFITHS & VAN SCHAIK, 1993; PEI, 1995; AKABAR & GORMAN, 1996; VAN SCHAIK & GRIFFITHS, 1996; MIURA *ET AL*,. 1997; BLANCHONG & SMALE, 2000; JAYASEKARA *ET AL.*, 2003; O'BRIEN *ET AL.*, 2003; YASUDA, 2004). Such systems have proven useful for investigating activity patterns because one of the advantages of automatic camera systems is that they rarely disturb focal animals (OSTERBERG, 1962; CARLEY *ET AL.*, 1970; VAN SCHAIK & GRIFFITHS, 1996; CUTLER & SWANN, 1999).

By using automatic camera systems baited with fruit, we have elucidated the relationship between fruits characteristics and frugivores on the forest floor of a tropical seasonal forest in Thailand, which has distinct rainy and dry seasons. As a result, we accumulated considerable data on the activity patterns of many animal species. In this paper, firstly we describe the diel foraging activity patterns of frugivorous or omnivorous animals inhabiting the tropical seasonal forest of Khao Yai National Park, Thailand. We then investigate the presence or absence of any seasonal changes in the activity patterns of these species.

STUDY AREA

The studies were conducted from July 2000 to June 2002 in Khao Yai National Park (hereafter KY, Fig. 1). The park lies between the latitudes of 14°05'–15'N and the longitudes of 101°05'–50'E in the Dongruk mountain range, and covers an area of 2,168 km^2. Its elevation ranges from 250 to 1,351 m. The principal study area was located near the headquarters of the National Park and covers approximately 70 km^2 (KITAMURA *ET AL.*, 2002, 2005, SMITINAND, 1977 for a detailed description). The study area ranged from 600 to 800 m asl in elevation and was mainly covered with moist evergreen forest which covers approximately 64% of the total park area and extends between 400 and 1,000 m asl (SMITINAND, 1977). The mean annual rainfall is 2,340 mm (1993–2003) with the rainy season usually occurring from April to October and the dry season from November to March (KITAMURA *ET AL.*, 2004). The mean monthly temperature ranges from 21°C

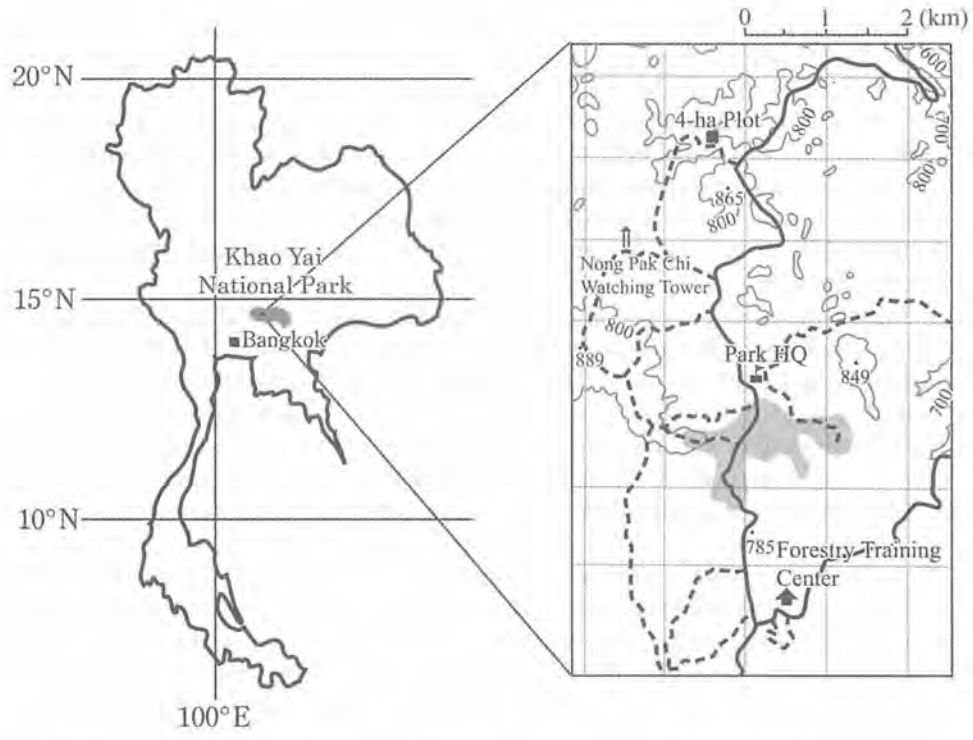

Figure 1. Location of Khao Yai National Park

(December and January) to 32°C (April and May). Although ripe fruits (e.g. *Ficus* spp.) are available year-round (POONSWAD *ET AL.*, 1998), fruit diversity and abundance are relatively high in the rainy season and becoming scarce at the beginning of the dry season (BARTLETT, 2003).

METHODS

Automatic Camera System

We used two kinds of automatic camera systems. One consisted of a far-infrared sensor and motor-driven compact camera with a built-in timepiece. The details of this system are described in MIURA *ET AL.* (1997). Since April 2001, we have used another system consisting of a compact camera with a built-in infrared motion sensor (Sensor Camera "FIELDNOTE", MARIF Co. Ltd, Japan). The details of this system are described in YASUDA (2004). Camera systems were set in various habitats including primary forest, secondary forest, and the edge of forest. Five to 50 fruits that had been collected from the ground around parent trees were set at the base of the same trees as bait, and cameras were placed approximately 2 m away from the bait. When fruits were consumed by animals or

damaged by insects or microbes, they were replaced with new samples. Photography was continued for at least 5 consecutive days. The cameras were checked at intervals of one to three days, and films and batteries were replaced if necessary.

In total, 187 individual plants of 69 species were studied (Appendix 1). We collected all plants not identified in the field and assigned a temporary code. Plant specimens were later identified by experts and/or compared with those identified specimens deposited in the Forest Herbarium in Bangkok (BKF) and then revised according to the International Plant Name Index on the web site <http://www.ipini.org/index.html>. These specimens are kept in our laboratory in Khao Yai National Park.

Based on the pictures, we were able to determine when and which animal species visited the fruit baits. We followed SRIKOSAMATARA & HANSEL (1996) with partial modifications by CORBET & HILL (1992) for the taxonomic nomenclature of mammals, and followed LEKAGUL & ROUND (1991) for that of birds. Identifying small mammals based solely on pictures might be difficult. However, we have conducted trapping of small mammals in order to study their population dynamics in KY (SUZUKI *ET AL.*, unpublished data). Thus, we were able to identify small mammals by comparing those in the pictures with those that had been trapped using their body size and color.

Since the cameras were triggered continuously if an animal or a group of animals stayed within the detection area of the sensor, one picture did not necessarily represent a single visit by a given animal. To overcome this problem, we followed O'BRIEN (2003) and YASUDA (2004) who regarded a picture as indicating a single visit by a given species if the picture was taken more than 30 minutes after the last picture of that species.

Classification of Animals Based on Activity Patterns

Activity patterns were analyzed for each species by accumulating hourly visits for the duration of the study period. Therefore, a variable number of individuals contributed to the data of a given species.

The study period was divided into rainy (April to October) and dry (November to March) seasons. Differences in the diel activity patterns between the rainy and dry seasons were tested using the Kolmogorov-Smirnov two-sample test. This analysis was performed for animal species for which 40 or more visits were recorded in both rainy and dry seasons because at least 40 samples are needed for this test. If there was no significant difference between rainy and dry seasons, the data were pooled for further analyses.

In the present study area, the time of sunrise changes between 0545 and 0643 h over the year, and that of sunset between 1743 and 1847 h. According to the standard time near KY, we divided a day into the following three time zones: daytime from 0700 to 1700 h; nighttime from 1900 to 0500 h; crepuscular time from 0500 to 0700 h and 1700 to 1900 h.

Based on the temporal distribution of visits, animal species were classified into the following three categories: (1) diurnal species, which had never visited fruit baits in the nighttime; (2) nocturnal one, which had never visited the fruit baits in the daytime; and (3) the others, which had visited the fruit baits during both daytime and nighttime. This classification was applied to animal species for which 30 or more visits had been recorded, as 30 or more visits were required for statistically testing activity patterns (see below for further explanation).

The chi-square test was performed for the activity patterns obtained for each species with the null hypothesis that all visits occurred at random independent of the time of day. Under this null hypothesis, the expected visit rates are 10/24, 10/24 and 4/24 for the daytime, nighttime and crepuscular time, respectively. Since the determination of chi requires that the expected value for the crepuscular time (4/24) exceeds 5, a total of 30 or more visits were required.

RESULTS

Animal Species Photographed

We obtained a total of 11,133 pictures containing animals. Forty-eight animal species could be identified for 10,955 pictures (98.4% of all pictures), and the time at which the photograph was taken was also recorded. The photographed animals included 30 species of mammals, 17 birds, and 1 reptile (Table 2 and Appendix 2). Mammal species accounted for 89.6% of all animals identified in the pictures, which included one species of Scandentia, 1 Insectivora, 1 Primate, 14 Carnivora, 1 Proboscidae, 4 Artiodactyla, and 8 Rodentia. Several chiropteran species were also photographed in 9 pictures, but these could not be identified to species.

Of the taxa that were identified to species, the yellow rajah rat (*Maxomys surifer*) was the most frequently photographed (3,318 pictures), followed by the pig-tailed macaque (*Macaca nemestrina*; 1,665) and the Indochinese ground squirrel (*Menetes berdmorei*; 1,073). The pictures with these 3 species accounted for 55.6% (6,056 pictures) of all the pictures. Conversely, 12 species of mammals, one species of reptile, and 6 species of birds were photographed less than 10 times. Carnivora tended to be photographed infrequently, and 9 of 14 Carnivora species were photographed less than 10 times.

After omitting pictures of the same species that were taken after an interval of less than 30 min, 4,819 of 10,955 pictures (44.0%) were regarded as representing a new visit for a given species and used for further analyses.

Seasonal Change of Activity Patterns

The animal species for which 40 or more visits were recorded in both the rainy and dry seasons are listed in Table 1 (see also Table 2 for the activity patterns). There were significant differences in the temporal distribution of visits between the rainy and dry seasons for the Malayan porcupine (*Hystrix brachyura*), the Siamese fireback (*Lophura diardi*) and the red jungle fowl (*Gallus gallus*) (Kolmogorov-Smirnov two-sample test, $P < 0.05$; Table 1, Fig. 2).

In the rainy season, *H. brachyura* exhibited unimodal activity patterns with a plateau at between 2100 and 0200 h. However, in the dry season, activity in this species was bimodal with peaks just after dusk and just before dawn (Fig. 2a). *Lophura diardi* exhibited almost entirely bimodal activity in both the rainy and dry seasons, but the morning peak was slightly greater than the afternoon peak in the rainy season, but smaller in the dry season (Fig. 2b). *Gallus gallus* also exhibited bimodal activity with distinct peaks in the early morning and the late afternoon in the rainy season, whereas the morning peak was

Table 1. The results of Kolmogorov-Smirnov two-sample test for the species for which 40 visits or more were recorded in both the rainy and dry seasons. Total, the total number of visits; Rainy, the number of visits in the rainy season; Dry, the number of visits in the dry season; ns, not significant; *, $p<0.05$; **, $p<0.01$.

Species name	English name	Total	Rainy	Dry	D	P
Macaca nemestrina	Pig-tailed macaque	350	233	117	0.085	ns
Muntiacus muntjak	Barking deer	259	135	124	0.078	ns
Cervus unicolor	Sambar deer	139	57	82	0.182	ns
Menetes berdmorei	Indochinese ground squirrel	527	396	131	0.049	ns
Niviventer fulvescens	Chestnut rat	194	60	134	0.139	ns
Maxomys surifer	Yellow rajah rat	2081	1500	581	0.022	ns
Hystrix brachyura	Malayan porcupine	216	152	64	0.291	**
Lophura diardi	Siamese fireback	219	106	113	0.198	*
Gallus gallus	Red junglefowl	112	67	45	0.274	*

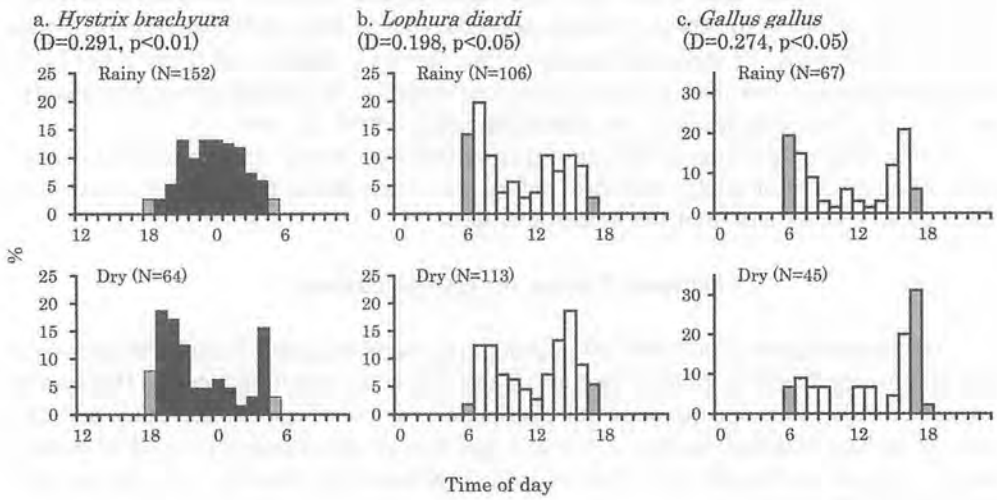

Figure 2. Activity patterns of the animals that exhibited significant seasonal changes in behavior. Abscissa, time of day; ordinate, the rate (%) of visits for each hour. Top, rainy season, from April to October; bottom, dry season, from November to March. Open column, daytime; gray column, crepuscular time; closed column, nighttime.

obscured in the dry season (Fig. 2c).

In the other 5 species, activity patterns were not significantly different between rainy and dry seasons (Kolmogorov-Smirnov two-sample test, $P > 0.05$). Thus, for these species, the data for the duration of the study period were combined for further analyses.

Diel Activity Pattern of Each Species

The 18 species for which 30 or more visits were recorded are classified into three categories (Table 2; see Appendix 2 for the data of the species for which less than 30 visits were recorded). Four mammal and all of the 6 bird species are regarded as diurnal. These diurnal species may be further classified into two subcategories; one (D–1) containing species that had almost unimodal activities with either a distinct or a vague peak around noon or afternoon, and the other (D–2) containing species that were primarily bimodally active with distinct peaks in the morning and late afternoon. The former subcategory, D–1, contained 2 mammals (*M. nemestrina* and *Callosciurus finlaysonii*) and 3 bird species (*Chalcophaps indica, Pitta cyanea* and *Garrulax leucolophus*, Fig. 3). Approximately 90% of the members of both of these groups were recorded in the daytime (Table 2). Of these, *M. nemestrina* (Fig. 3a) and *C. indica* (Fig. 3c) were recorded most frequently around noon whereas *C. finlaysonii* (Fig. 3b) and two bird species (*P. cyanea* (Fig. 3f) and *G. leucolophus* (Fig. 3e)) were photographed more frequently in the afternoon. The latter subcategory, D–2, contained 2 mammals (*Tupaia belangeri* (Fig. 4a) and *M. berdmorei* (Fig. 4b)) and 3 bird species (*L. diardi* for both seasons (Fig. 2b), *G. gallus* for both seasons (Fig. 2c), and *Arborophila chloropus* (Fig. 4c)). This bimodal activity pattern was particularly conspicuous in the two mammal species, and more than 50% of their visits were recorded in the crepuscular time (Table 2).

Five rodent species (*Rattus* spp., *Niviventer fulvescens, Leopoldamys sabanus, Maxomys surifer*, and *H. brachyura* for both the rainy and dry seasons) were regarded as nocturnal (Figs. 2a, and 5), with more than 90% of the visits for these species being recorded in the nighttime. Three rat species (*Rattus* spp., *N. fulvescens* and *M. surifer*) exhibited peaks in visiting frequency during the first hour of nighttime between 1900 and 2000 h.

Three artiodactyl species were recorded during both day and night (Fig. 6). *Tragulus javanicus* (Fig. 6a) and *Muntiacus muntjak* (Fig. 6c) were active mainly during day with peaks around the dawn and dusk, whereas *Cervus unicolor* (Fig. 6b) was active mainly at night although it was also photographed during the day.

In all species for which 30 visits or more were recorded, the temporal distributions of visits were significantly different from the pattern expected from the null hypothesis (Table 2, Chi-square test, $P < 0.05$).

DISCUSSION

Comparison with Previous Studies

There have been relatively few studies that have investigated the activity patterns of multiple animal species coexisting in tropical forests (VAN SCHAIK & GRIFFITHS 1996; MIURA *ET AL.* 1997). VAN SCHAIK & GRIFFITHS (1996) studied the activity patterns of 31

Table 2. Activity patterns of the species for which 30 or more visits were recorded. Pictures, total number of pictures; total visits, total number of visits; Daytime, number of visits recorded during the daytime; Crepuscular time; number of visits recorded during the crepuscular time; Nighttime, number of visits recorded during nighttime. Percentages of the total number of visits are shown in the parentheses. Abbreviations for the categories of activity patterns are as follows: D–1, diurnal with unimodal distribution; D–2, diurnal with bimodal distribution; N, nocturnal; O, others. ***, $P < 0.001$ for χ^2 test.

Family	Species name	English name	Pictures	Total visits	Daytime time	Crepuscular			Nighttime		χ^2	P	Category	
Scandentia Tupaiidae	*Tupaia belangeri*	Northern tree shrew	190	121	54	(45)	67	(55)	0	(0)	75.7	***	D–2	Primates
Cercopithecidae	*Macaca nemestrina*	Pig-tailed macaque	1665	350	320	(91)	27	(8)	0	(0)	224.3	***	D–1	Artiodactyla
Tragulidae	*Tragulus javanicus*	Lesser Malay mouse-deer	177	96	51	(53)	42	(44)	3	(3)	44.8	***	O	
Cervidae	*Cervus unicolor*	Sambar	321	139	7	(5)	25	(18)	107	(77)	54.6	***	O	
	Muntiacus muntjak	Barking deer	938	259	142	(55)	63	(24)	54	(21)	26.3	***	O	Rodentia
Sciuridae	*Callosciurus finlaysonii*	Finlayson's squirrel	305	106	99	(93)	7	(7)	0	(0)	69.8	***	D-1	
	Menetes berdmorei	Indochinese ground squirrel	1073	527	209	(39)	318	(61)	0	(0)	350.4	***	D–2	
Muridae	*Rattus* spp.		85	63	0	(0)	3	(5)	60	(95)	43.6	***	N	
	Niviventer fulvescens	Chestnut rat	242	194	0	(0)	17	(9)	177	(91)	121.5	***	N	
	Leopoldamys sabanus	Noisy rat	120	73	0	(0)	0	(0)	73	(100)	60.1	***	N	
	Maxomys surifer	Yellow rajah rat	3318	2081	0	(0)	134	(6)	1947	(94)	1375.7	***	N	
Dipodidae	*Hystrix brachyura* (Rainy)	Malayan porcupine	772	152	0	(0)	8	(5)	144	(95)	103.7	***	N	
	H. brachyura (Dry)		329	64	0	(0)	7	(11)	57	(89)	38.4	***	N	Birds
Galliformes Phasianidae	*Lophura diardi* (Rainy)	Siamese fireback	219	106	88	(83)	18	(17)	0	(0)	58.7	***	D–2	
	L. diardi (Dry)		208	113	105	(93)	8	(7)	0	(0)	73.5	***	D–2	
	Gallus gallus (Rainy)	Red junglefowl	108	67	50	(75)	17	(25)	0	(0)	35.4	***	D–2	
	G. gallus (Dry)		101	45	27	(60)	18	(40)	0	(0)	24.6	***	D–2	
	Arborophila chloropus	Scaly-breasted partridge	62	40	27	(68)	13	(33)	0	(0)	21.2	***	D–2	
Columbiformes														
Columbidae	*Chalcophaps indica*	Emerald dove	130	100	97	(97)	3	(3)	0	(0)	73.2	***	D–1	
Passeriformes Pittidae	*Pitta cyanea*	Blue pitta	42	31	27	(87)	4	(13)	0	(0)	18.0	***	D–1	
Muscicapidae	*Garrulax leucolophus*	White-crested laughingthrush	65	46	43	(93)	3	(7)	0	(0)	30.3	***	D–1	

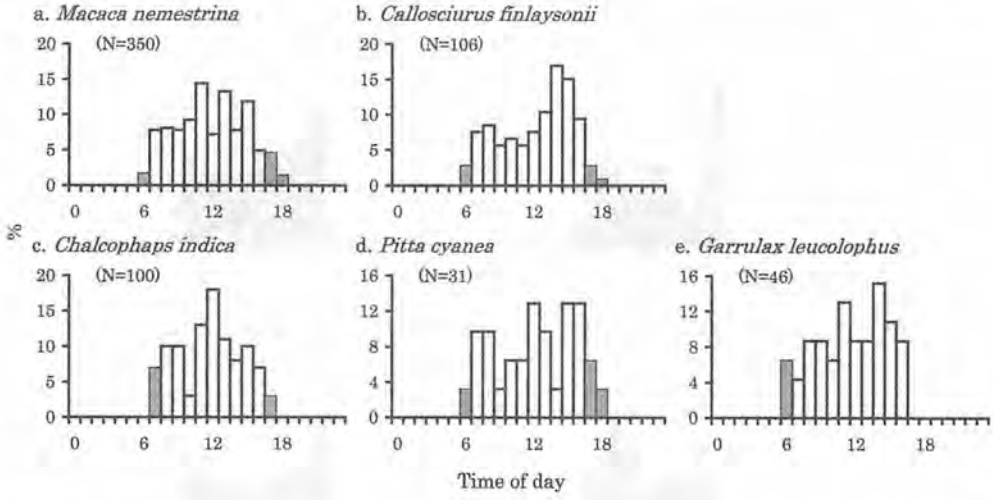

Figure 3. Activity patterns of the animals classified as diurnal species with an almost unimodal distribution. See Fig. 2 for further explanations.

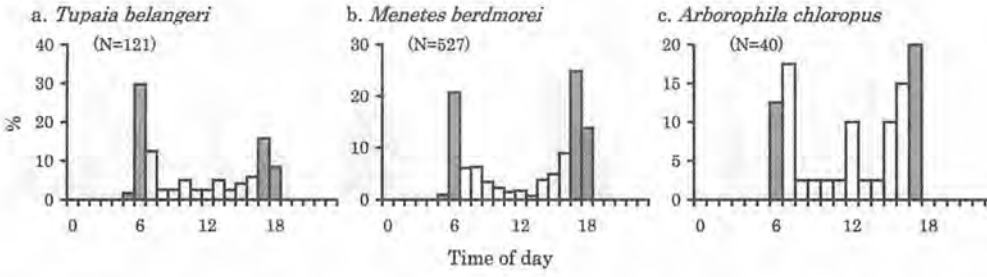

Figure 4. Activity patterns of the animals classified as diurnal species with a bimodal distribution. See Fig. 2 for further explanations.

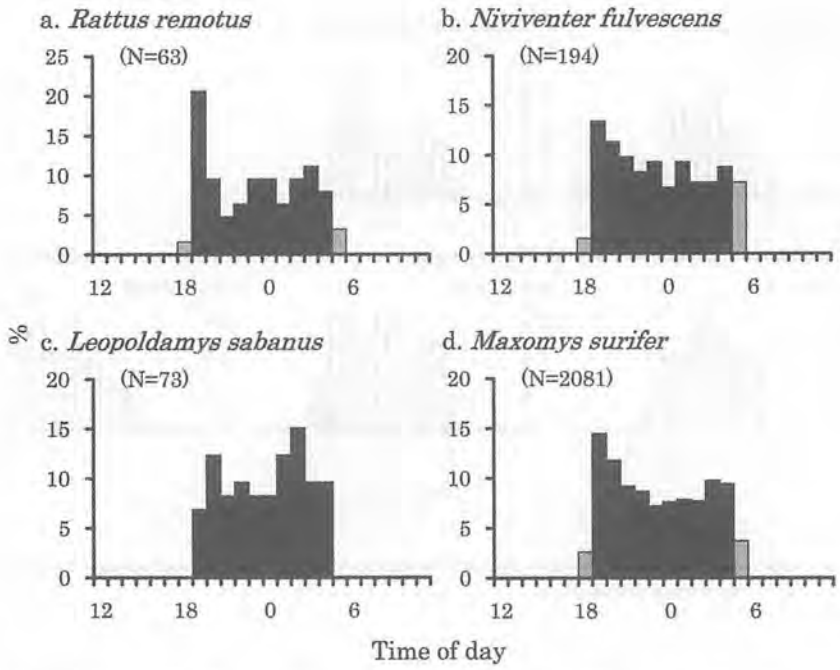

Figure 5. Activity patterns of the animals classified as nocturnal species. See Fig. 2 for further explanations.

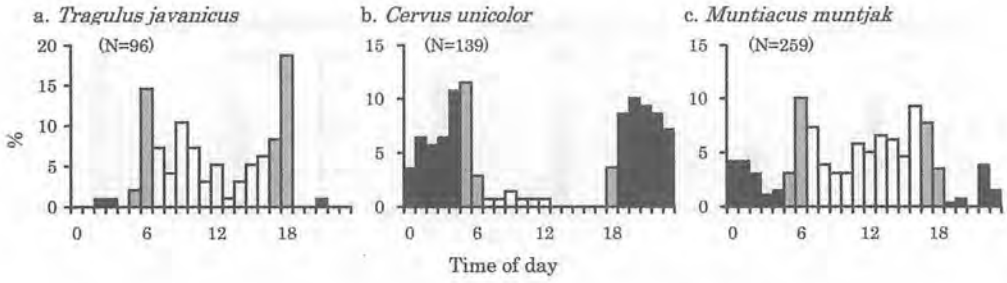

Figure 6. Activity patterns of the animals classified as being active during both the day and night. See Fig. 2 for further explanations.

animals in Indonesian rain forests using automatic camera systems. They classified the photographed animals into the following categories: diurnal, nocturnal and cathemeral (the last category had been defined by TATTERSALL (1987) for primates as being active during both day and night). In addition, they showed that arboreal species were either strictly diurnal or nocturnal, whereas terrestrial species were primarily cathemeral. However, their results do not appear so convincing because their sample sizes were relatively low (1,308 pictures in total) and most species (20 of 31 species) were photographed less than 20 times. Furthermore, the time at which the pictures were actually taken did not appear to be recorded on their pictures by their camera systems. Consequently, the activity patterns described by VAN SCHAIK & GRIFFITHS (1996) do not appear to be so accurate.

By using automatic camera systems, MIURA *ET AL.* (1997) showed the activity patterns of animals in a tropical rain forest of the Malay Peninsula by taking 2,738 pictures on which the time of the animal visiting was printed. They described the activity patterns of 8 representative mammal species, 3 of which were nocturnal, 3 were diurnal and 2 were active irrespective of day and night.

In the present study, we took a considerable number of pictures (in excess of 10,000). In addition, we considered only those pictures taken 30 minutes or more after the previous picture as constituting an independent visit. In doing so, we believe our results to be more reliable than those of previous studies.

Based on the standard time around KY, we divided a day into the following three parts; daytime, nighttime, and crepuscular time. While the definition of crepuscular time may not be precise given that the timing of sunset and sunrise changed seasonally (although the change was remained less than one hour), the activity patterns of the frequently photographed animal species could be classified without difficulty (Figs. 2–6; Table 2). Below we discuss the activity patterns of species belonging to each category.

Diurnal species

The 2 mammal species and the 3 bird species were classified into the subcategory of D–1 (diurnal with a peak or peaks around noon or afternoon, Fig. 3). Of these, the 2 mammals share a rather arboreal tendency. Furthermore, in the 3 birds, all of which belong to Columbiformes or Passeriformes, the tendency to stay on the ground appears to be weak when compared to the birds in subcategory D–2, all of which belong to Phasianidae (see below).

The 2 mammals and the 3 phasianids classified as D–2 (diurnal with peaks in the early morning and late afternoon) share a tendency of living mainly on the ground. In a tropical rain forest of Singapore, many invertebrates were observed to move from the shelter of the forest floor to the canopy to feed at around dusk and to return around dawn, when predators such as scorpions frogs and spiders ambushed and preyed on these invertebrates at the base of trees (WHITMORE, 1990). Tree shrews and ground squirrels are also known to frequently prey upon invertebrates as well as fruits (HARRISON, 1961; LEKAGUL & MCNEELY 1977; MACKINNON, 1978; CORBET & HILL, 1992; MACKINNON *ET AL.*, 1996; EMMONS, 2000). The birds of the Phasianidae also appear to eat invertebrates. Consequently, it is hypothesized that the bimodal activity pattern of the D–2 species in KY may be related to a habit of preying on invertebrates on the forest floor.

Nocturnal species

In the present study, all 4 of the Muridae species and the Malayan porcupine, *Hystrix brachyura*, were nocturnal (Figs. 2a, b, and 5; Table 2). In the 3 murid species, *Maxomys surifer, Niviventer fulvescens* and *Rattus* spp., and the Malayan porcupine, activity started in the late dusk after 1800 h and ceased in the early dawn before 0600 h, *Leopoldamys sabanus*, however, became active after 1900 h in the early at nighttime and ceased before 0500 h.

PEI (1995) studied the activity pattern of the spinous country rat, *Niviventer coxingi*, using an automatic camera system in Taiwan and suggested that the onset and cessation of its activities were controlled by rapid changes in light intensity accompanying sunset and sunrise. Similar regulation of activity was reported by CARLEY *ET AL.* (1970) for the deer mouse, *Peromyscus maniculatus*, in Kansas, USA. The onset and cessation of activities of the nocturnal species observed in the present study may also be controlled by light intensity. If so, the present results suggest that the light intensities under which *L. sabanus* becomes active may be lower than those for the other 4 nocturnal species.

Other species

The 3 species of Artiodactyla in KY, *Tragulus javanicus, Cervus unicolor,* and *Muntiacus muntjak,* were active during both day and night (Fig. 6); these species may be regarded as cathemeral as defined by TATTERSALL (1987). These results agree with those of previous studies conducted in Southeast Asia (VAN SCHAIK & GRIFFITHS 1996; MIURA *ET AL.*, 1997; MCCULLOUGH *ET AL.*, 2000). MATSUBAYASHI *ET AL.*, (2003) reported that the mouse deer, *T. javanicus*, was observed to wander or forage on the forest floor only during the daylight periods (0500–1900 h), and that it moved between foraging and resting sites at dawn and dusk in the Kabili-Sepilok Forest Reserve in Sabah, Borneo. MIURA *ET AL.* (1997) also reported that *T. javanicus* was active irrespective of day and night in Pasoh, the Malay Peninsula. Conversely, SRIKOSAMATARA & HANSEL (1996) regarded *T. javanicus* in KY as being primarily nocturnal (although it was also active during the daytime, particularly in the dry season). In the present study, however, *T. javanicus* was recorded mainly during the day (0600–1800 h), with peaks in the morning and evening (Fig. 6c). Thus, the present results are in agreement with those for other reserves of Pasoh (MIURA *ET AL.*, 1997) and Sabah (MATSUBAYASHI *ET AL.*, 2003).

In the present study, as well as that of MIURA *ET AL.* (1997), fruit was used as bait. Therefore, most species observed in the present study were considered to be either frugivorous or omnivorous animals (although several carnivores were also infrequently recorded). Furthermore, the activities recorded in the present study were considered to be directed primarily at foraging. It is important to note that the present results may be limited by the fact that activities other than foraging may have been missed. Further studies using other methods will therefore be required in order to assess the activity patterns of each species more comprehensively.

Seasonal Changes in Activity Patterns

There were significant differences in the activity patterns between the rainy and dry seasons for the 3 species (the porcupine, *Hystrix brachyura*, and the 2 birds *Lophura diardi* and *Gallus gallus*) of the 9 species investigated concerning seasonal change (Table 1. and

Fig. 2). In all 3 species, the activity patterns of both the rainy and dry seasons were classified into the same category (Table 2). However, in *H. brachyura* the temporal distribution of visits was markedly different between the rainy and dry seasons; a plateau was observed around midnight in the rainy season whereas peaks just after dusk and just prior to dawn were seen in the dry season (Fig. 2a). At present, we have no explanation for these changes in activity pattern between the rainy and dry seasons.

In both of the bird species (*L. diardi* and *G. gallus*), morning activity appeared to be more vigorous in the rainy season (Figs. 2b and 2c). However, it is also unclear whether this seasonal change in behavior is an adaptation to seasonal changes in some environmental factors.

We have described the diel foraging activity patterns of frugivorous and omnivorous animals on the forest floor and described seasonal changes in the foraging behavior of several species for the first time in a tropical seasonal forest. The adaptive significance of the seasonal changes remains unclear; they may be affected by physiological constraints and/or environmental factors such as the availability of food items. Moreover, although fruit was used as bait in the present study, some carnivores such as the leopard cat (*Prionailurus bengalensis*) and dhole (*Cuon alpinus*) were infrequently recorded (Appendix 2). It remains unclear whether they came to take fruits or to hunt the frugivorous or omnivorous animals that visited the baited sites. However, their activity may influence the time when the frugivores or omnivores are active. Further studies on the ecology and behavior of each species, including the carnivores, are required in order to understand the variety of factors that determine the changes in diel and seasonal activity patterns of forest animals.

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Appendix 1. List of plant species used as bait and the number of days when camera-traps operated on each plant species.

Family	Species Name	Trap days
Anacardiaceae	*Choerospondias axillaris*	295
Annonaceae	*Alphonsea* sp.SK095	35
	Dasymaschalon sootepense	26
	Desmos chinensis	4
	Miliusa cuneata	27
	Platymitra macrocarpa	136
	Polyalthia sp.SK115	19
	Polyalthia sp.SK195	37
	Polyalthia sp.	24
	Uvaria lurida	12
Burseraceae	*Canarium euphyllum*	189
Celastraceae	*Bhesa robusta*	32
Cornaceae	*Mastixia pentandra*	103
Cucurbitaceae	*Trichosanthes tricuspidata*	68
Dipterocarpaceae	*Dipterocarpus gracilis*	53
Ebenaceae	*Diospyros glandulosa*	21
Elaeagnaceae	*Elaeagnus conferta*	90
Elaeocarpaceae	*Elaeocarpus robustus*	104
Euphorbiaceae	*Balakata baccata*	65
	Macaranga siamensis	36
	Euphorbiaceae sp.SK256	14
Fagaceae	*Lithocarpus* sp.	41
	Lithocarpus thomsonii	23
	Quercus myrsinaefolia	125
Flacourtiaceae	*Casearia grewiifolia*	58
	Casearia sp.	10
Gnetaceae	*Gnetum* sp.SK024	39
Guttiferae	*Garcinia* sp.SK442	17
Icacinaceae	*Gonocaryum lobbianum*	34
	Platea latifolia	60
Lauraceae	*Beilschmiedia* sp.SK437	23
	Beilschmiedia maingayi	5
	Cinnamomum subavenium	106
	Cryptocarya sp.SK424	54
	Phoebe cathia	24
Leguminosae	*Acacia* sp.SK398	127
	Acrocarpus fraxinifolius	23
	Entada rheedii	26
Magnoliaceae	*Michelia baillonii*	18
Meliaceae	*Aglaia lawii*	44
	Aglaia spectabilis	186
	Aphanamixis polystachya	12
	Dysoxylum cyrtobotryum	37
	Melia azedarach	103
	Sandoricum koetjape	91
Moraceae	*Antiaris toxicaria*	50
	Artocarpus lacucha	31
	Ficus altissima	136
	Ficus annulata	39
	Ficus kurzii	27
	Ficus subcordata	119
	Ficus sp.2	2
	Ficus sp.3	12
Myricaceae	*Knema elegans*	18
	Syzygium albiflorum	52
	Cleistocalyx nervosum	26
Palmae	*Areca triandra*	69
	Livistona jenkinsiana	25
Proteaceae	*Helicia formosana*	20
Rubiaceae	*Anthocephalus chinensis*	133
	Nauclea sp.SK033	85
	Canthium coffeoides	47
Rutaceae	*Acronychia pedunculata*	14
	Citrus limon	7
	Citrus sp.	62
	Clausena harmandiana	43
Sapindaceae	*Mischocarpus pentapetalus*	31
Sapotaceae	*Pouteria stellibacca*	73
Ulmaceae	*Aphananthe cuspidata*	59

Appendix 2. Species for which less than 30 visits were recorded. See Table 2 for further explanation.

	Family	Species name	English name	Pictures	Total visits	Day time		Crepuscular time		Night time	
Insectivora	Crocidurinae	*Crocidura horsfieldi*	Horsfield's shrew	1	1	0	(0)	0	(0)	1	(100)
Chiroptera			Bat	9	9	2	(22)	0	(0)	7	(78)
Carnivora	Canidae	*Cuon alpinus*	Dhole	32	6	5	(83)	1	(17)	0	(0)
	Ursidae	*Ursus thibetanus*	Asiatic black bear	12	7	1	(14)	0	(0)	6	(86)
		U. malayanus	Sun bear	2	2	1	(50)	1	(50)	0	(0)
	Mustelidae	*Martes flavigula*	Yellow-throated marten	2	2	2	(100)	0	(0)	0	(0)
		Arctonyx collaris	Hog-badger	2	2	1	(50)	0	(0)	1	(50)
		Viverra zibetha	Large Indian civet	24	17	0	(0)	4	(24)	13	(76)
		V. megaspila	Large spotted civet	1	1	0	(0)	0	(0)	1	(100)
		Viverricula indica	Small indian civet	9	5	0	(0)	1	(20)	4	(80)
		Paradoxurus hermaphroditus	Common palm civet	53	28	0	(0)	5	(18)	23	(82)
	Herpestidae	*Herpestes javanicus*	Small asian mongoose	6	4	4	(100)	0	(0)	0	(0)
	Felidae	*Prionailurus bengalensis*	Leopard cat	35	19	2	(11)	6	(32)	11	(58)
		Catopuma temminckii	Golden cat	2	2	0	(0)	1	(50)	1	(50)
		Pardofelis nebulosa	Clouded leopard	2	1	0	(0)	0	(0)	1	(100)
		P. marmorata	Marbled cat	5	2	2	(100)	0	(0)	0	(0)
Proboscidea	Elephantidae	*Elephas maximus*	Asian elephant	41	9	3	(33)	5	(56)	1	(11)
Artiodactyla	Suidae	*Sus scrofa*	Wild boar	36	24	5	(21)	6	(25)	13	(54)
Rodentia	Dipodidae	*Atherurus marourus*	Asiatic brush-tailed porcupine	2	1	0	(0)	0	(0)	1	(100)
Reptile	Varanidae	*Varanus salvator*	Monitor lizard	1	1	1	(100)	0	(0)	0	(0)
Bird	Phasianidae	*Lophura nycthemera*	Silver pheasant	21	10	10	(100)	0	(0)	0	(0)
Galliformes											
Cuculiformes	Cuculidae	*Carpococcyx renauldi*	Coral-billed ground-cuckoo	29	24	21	(88)	3	(13)	0	(0)

Appendix 2. Species for which less than 30 visits were recorded. See Table 2 for further explanation. (Cont.)

	Family	Species name	English name	Pictures	Total visits	Day time		Crepuscular time		Night time	
Coraciiformes	Bucerotidae	*Anthracoceros albirostris*	Oriental pied hornbill	100	22	22	(100)	0	(0)	0	(0)
Passeriformes	Pittidae	*Pitta phayrei*	Eared pitta	1	1	1	(100)	0	(0)	0	(0)
	Pycnonotidae	*Criniger pallidus*	Puff-throated bulbul	29	19	19	(100)	0	(0)	0	(0)
	Muscicapidae	*Garrulax chinensis*	Black-throated laughingthrush	2	2	2	(100)	0	(0)	0	(0)
		Luscinia cyane	Siberian blue robin	6	3	3	(100)	0	(0)	0	(0)
		Copsychus malabaricus	White-rumped shama	1	1	1	(100)	0	(0)	0	(0)
		Monticola solitarius	Blue rock-thrush	1	1	1	(100)	0	(0)	0	(0)
		Zoothera citrina	Orange-headed thrush	17	11	11	(100)	0	(0)	0	(0)
		Cyornis sp.	Blue flycatcher	1	1	1	(100)	0	(0)	0	(0)