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EVIDENCE FOR FOOD HOARDING BEHAVIOUR IN TERRESTRIAL RODENTS IN PASOH FOREST RESERVE, A MALAYSIAN LOWLAND RAIN FOREST

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YASUDA, M., MIURA, S. & NOR AZMAN, H. 2000. Evidence for food hoarding behaviour in terrestrial rodents in Pasoh Forest Reserve, a Malaysian lowland rain forest. Food hoarding behaviour of terrestrial rodents in a Malaysian forest was studied using a thread-marking method and automatic camera system. The fruit of an introduced palm species, *Elaeis guineensis* (oil palm), was used as bait for the experiment. Two types of scatter hoarding were recognised: 1) nocturnal rats *Leopoldamys sabanus* and *Maxomys* spp. cached fruit on the ground covered with leaves (93% and 100% of stored fruit respectively), 2) the diurnal ground squirrel *Lariscus insignis* cached fruit in soil (82%). Mean distances from a feeding platform to caches made by *Leopoldamys sabanus* and *Lariscus insignis* were 16.1 m ± 1.44 s.e. (n = 30, range 0.4–29.4 m) and 15.3 m ± 2.10 s.e. (n = 11, range 5.2–32.7 m) respectively. The longevity of caches was short: 37 of 47 caches (78.7%) were retrieved within a day. The evidence for hoarding behaviour among terrestrial rodents is the first ever reported from Malaysian rain forests.

Key words: Hoarding behaviour - scatter hoarding - seed dispersal - *Leopoldamys sabanus* - *Lariscus insignis* - *Maxomys* spp. - Pasoh Forest Reserve

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YASUDA, M., MIURA, S. & NOR AZMAN, H. 2000. Bukti tabiat penyorokan makanan bagi rodensia darat di Hutan Simpan Pasoh, sebuah hutan hujan tanah pamah di Malaysia. Tabiat menyorok makanan bagi rodensia darat di hutan di Malaysia dikaji menggunakan kaedah penandaan benang dan sistem kamera automatik. Buah daripada spesies palma yang diperkenalkan, *Elaeis guineensis* (kelapa sawit), digunakan sebagai umpan dalam ujian ini. Dua jenis sorokan secara berselerak telah dikenal pasti: 1) tikus malam, *Leopoldamys sabanus* dan *Maxomys* spp., menyembunyikan buah di atas tanah dengan menutupnya dengan daun-daun (masing-masing 93% dan 100% daripada buah yang disimpan), 2) tupai tanah siang, *Lariscus insignis*, menyembunyikan buah di dalam tanah (82%). Jarak purata dari tempat ia mengambil makanan ke tempat penyembunyian yang dibuat oleh *Leopoldamys sabanus* dan *Lariscus insignis* ialah 16.1 m ± 1.44 s.e. (n=30, berjulat 0.4–29.4 m) dan masing-masing 15.3 m ± 2.10 s.e. (n=11, berjulat 5.2–32.7 m). Masa penyembunyian adalah pendek: 37 daripada 47 penyembunyian (78.7%) dapat ditemui dalam masa sehari. Bukti tabiat penyorokan di kalangan rodensia darat merupakan kes pertama yang pernah dilaporkan dari hutan di Malaysia.

Introduction

Food hoarding behaviour may allow animals to optimise foraging and feeding, and to improve chances of survival during food scarcity. Food hoarding is also of value to plants, since it aids in the dispersion of plant propagules (Howe & Westley 1988, Vander Wall 1990). Food hoarding is generally divided into scatter hoarding and larder hoarding. The former refers to the spatially scattered food caches made in the litter, humus or soil, and the number of hoarded items is small. The latter refers to clumped caches usually made in the respective animal's burrow, and a single cache may contain a relatively large number of food items (Vander Wall 1990).

Food hoarding behaviour is a common behaviour among rodents, both in the tropics and temperate regions. There have been several studies focusing on hoarding behaviour and its consequences for plants in neotropic (Smythe 1970, Forget 1990, 1993, Forget & Milleron 1991) and Afrotropical forests (Emmons 1980). These studies revealed that, through food hoarding, terrestrial rodents are often important seed dispersers. On the other hand, little evidence for such behaviour has been found in the forests of Southeast Asia (Terborgh 1990). MacKinnon (1978) and Becker *et al.* (1985) reported that some arboreal diurnal squirrels showed food hoarding behaviour at the canopy level. Of course, these arboreal squirrels may contribute to the seed dispersal of plants. However, secondary seed dispersal occurring on the forest floor is expected to be more important because most seeds are shed beneath or near the parent tree where the mortality of seeds and seedlings is sometimes considerably higher (Janzen 1970, Wright 1983, Howe *et al.* 1985, Schupp 1988a,b). The present paper is the first published report of the scatter hoarding behaviour in terrestrial rodents in Malaysian rain forests.

Materials and methods

Study site

The study was carried out at the Pasoh Forest Reserve, Negeri Sembilan, Peninsular Malaysia. The forest consists of approximately 2500 ha of lowland dipterocarp rain forest including primary and regenerating forests. The flora, forest structure, and other plant ecology have been described elsewhere (Kira 1978, Kochummen *et al.* 1990, Manokaran & LaFrankie 1990, Manokaran *et al.* 1992, Manokaran & Swaine 1994). The mammalian fauna was described by Kemper (1988). She reported the occurrence of 84 species from 11 mammalian orders.

The forest reserve is located in the driest region of the southern Malay Peninsula. The mean annual rainfall is about 1700 mm with two rainy and two dry seasons each year. The dry seasons usually occur in January and July, and rainfall is often less than 100 mm $month^{-1}$ (Malaysian Meteorological Service 1961–1990). This bimodal pattern of rainfall is typical in western and southwestern parts of the Malay Peninsula, though the dry season in the other regions of the Peninsula is more moderate (Dale 1954).

Methods

Experimental feeding trials were conducted 10 times each in primary forest and regenerating forest, from December 1994 to March 1995. We used fruit of the oil palm (*Elaeis guineensis*) as the experimental food (weight 14.5 g ± 0.26 s.e., n = 160). The fruit contains a large proportion of oil in both its pulp and kernel (Hartley 1977). In each experiment, 16 fruits were set in the morning (0900h at the local time) on a feeding platform (30 × 30 cm in area, 3 cm in height) placed on the forest floor. The feeding platforms were set 100 m or more apart from each other to avoid the same individual animals coming to feed.

Fruit removal from the feeding platform was recorded with an automatic camera system, consisting of a single-lens reflex camera (RICOH XR10-M with 35–70 mm zoom lens), a flash (SUNPAK Auto25SR), and an infrared sensor (DELCATEC PS15-B). An infrared sensor was hung over the feeding platform and connected to the camera with an electric cable, located about two meters apart from the feeding platform. The camera had an auto-quartz timepiece, so that the time of each visit by an animal would be printed on the photograph. Details of the camera system have been described in Miura *et al.* (1997). This camera system allowed us to monitor the experiments on a 24-h basis.

The thread-marking method was used to trace the individual fruits removed by animals: each fruit was attached to one end of a nylon thread (20 cm long) through its pulp, and a pink-coloured plastic tag with a serial number (20 × 50 × 0.15 mm, 0.2 g in weight; Suzuki-syouten, Hokkaido, Japan) was attached to another end of the thread. From the photographs taken by the camera system, the visiting animal that removed the fruit with a certain tag could be easily identified to species.

A search for removed fruit was made within a column of 50 m in radius and 3 m in height around the feeding platform on the forest floor every morning until all the fruits were removed from the feeding platform. Distance was measured from the feeding platform to detected food caches or to feeding sites (where only tags were left). The micro-environmental conditions of the cache site (e.g. buried in soil or left on the ground, depth of cache, vegetation coverage and materials nearby) were recorded. Examination of the detected caches was made daily. Each experimental trial was considered complete when all the fruits in the caches were retrieved by the animals.

Results

All the oil palm fruits disappeared from the feeding platform within two days after the onset of a trial, 65% of the fruits were removed within a day. Visiting animals identified from photographs and the number of fruits removed by these species are presented in Table 1. Since the composition of visiting animals did not differ greatly between the primary and regenerating forests, the results are shown all together. Only 15% (n = 24) of removed fruits were not recorded by the camera system, probably due to the movement of the visiting animals. They were either too fast or slow to be detected by the sensor.

Five terrestrial animals were identified as fruit consumers, while no arboreal animals visited the feeding platforms (Table 1). Two of these animals are nocturnal rats and another is diurnal squirrel. The long-tailed giant rat, *Leopoldamys sabanus* (Thomas), visited most frequently and accounted for 49.4% (n = 79) of removed fruits. The second most common species was the three-striped ground squirrel, *Lariscus insignis* (Cuvier), which removed 20.0% (n = 32) of the fruits. The third species was the spiny rat, *Maxomys* spp., either *M. rajah* (Thomas) or *M. surifer* (Miller), which we were unable to distinguish based on the photographs. *Maxomys* spp. removed only three fruits. Other fruit consumers were the short-tailed mongoose, *Herpestes brachyurus* Gray (family Herpestidae), and a pheasant, the crestless fireback, *Lophura erythropthalma* (Raffles) (family Phasianidae), which accounted for 10.6% (n = 17) and 3.1% (n = 5) respectively, of removed fruits. All of these animal species are common in the primary and regenerating forests in the Pasoh Forest Reserve (Kemper & Bell 1985, Kemper 1988, Yasuda 1998).

A total of 47 scatter hoarding caches (29.4% of total fruits removed) were located (Table 1). Each cache contained one fruit. Caches were made at the following locations: at open sites (n = 4), under the litter (n = 30), or in soil (n = 13). Six of them were close to tree buttresses. No cache was found above ground, but coloured tags were sometimes located in small trees (height < 3 m, n = 9). In total, we found 57 feeding sites (35.6% of total fruits removed) where coloured tags and fragments of fruits were scattered either on the ground or in small trees, which were considered to indicate fruit consumption at that location.

Two types of cache were recognised (Table 1). The first was those caches in which fruits were partially or fully buried in soil (27.7% of all caches, n = 13). Fruits were buried at most sites about 1 cm below the ground surface. The second

Table 1. Fruit consumers photographed using the automatic camera system and fate of fruit removed from feeding table

Family	Species	Cache: on the ground	(%)	Cache: in soil	(%)	Eaten	(%)	Not found	(%)	Total
Class Mammalia										
Order Rodentia										
Sciuridae	*Lariscus insignis*	2	(6.3)	9	(28.1)	6	(18.8)	15	(46.9)	32
Muridae	*Leopoldamys sabanus*	28	(35.4)	2	(2.5)	23	(29.1)	26	(32.9)	79
	Maxomys spp.	1	(33.3)	0	(0.0)	0	(0.0)	2	(66.7)	3
Order Carnivora										
Viverridae	*Herpestes brachyurus*	0	(0.0)	0	(0.0)	15	(88.2)	2	(11.8)	17
Class Aves										
Order Galliformes										
Phasianidae	*Lophura erythropthalma*	0	(0.0)	0	(0.0)	5	(100.8)	0	(0.0)	5
Unknown		3	(12.5)	2	(8.3)	8	(33.3)	11	(45.8)	24
Total		34	(21.3)	13	(8.1)	57	(35.6)	56	(35.0)	160

type of cache was when fruits were stored on the ground surface (72.3%, n = 34), and 88.2% (n = 30) of the fruits were covered with fallen leaves. All caches were considered to be established by terrestrial rodents, while neither the short-tailed mongoose nor the crestless fireback showed hoarding behaviour (Table 1). Among rodents, *Leopoldamys sabanus* usually stored fruits on the ground surface (28 of 30 caches, 93%), while *Lariscus insignis* tended to make caches in the soil (9 of 11 caches, 82%). There was a significant difference between the hoarding behaviours of the two species (Fisher's exact probability test, two-tailed, $p < 0.001$).

The longevity of caches was short: 37 of 47 caches (78.7%) were consumed, moved, or disappeared within a day. No caches remained intact for more than one week.

The distance between the feeding platform and caches for the fruit removed by *Leopoldamys sabanus* was 0.4–29.4 m (mean 16.1 m ± 1.44 s.e.), while that by *Lariscus insignis* was 5.2–32.7 m (mean 15.3 m ± 2.10 s.e.; Figure 1). There were no significant differences in cache distance between the two species (Mann-Whitney's U-test, two-tailed, $p > 0.6$).

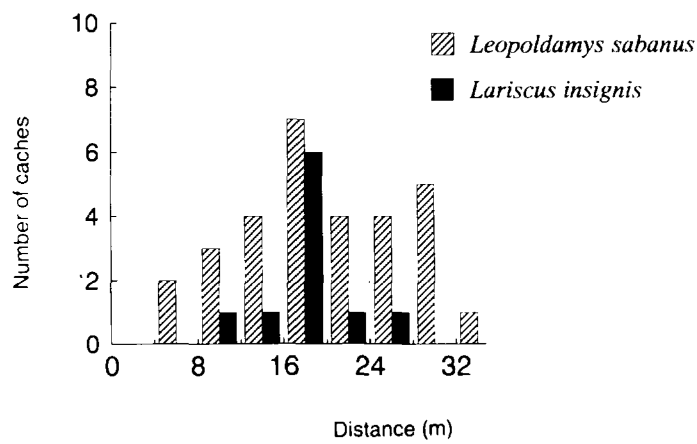

Figure 1. Distance of caches from feeding platform. Hatched bar: *Leopoldamys sabanus*, n = 30; black bar: *Lariscus insignis*, n = 11.

Discussion

This study revealed that *Leopoldamys sabanus, Maxomys* spp, and *Lariscus insignis* demonstrated scatter hoarding behaviour (Table 1). This is the first report of such behaviour in terrestrial rodents in Malaysian forests and perhaps in South-east Asian tropical forests. However, Medway (1983) observed that *Maxomys surifer* stored food in its nest, which suggests that it shows both scatter and larder hoarding behaviour.

These three rodents that demonstrated scatter hoarding behaviour have a wide distribution, ranging from lowland to hill forests (Lim 1970, Langham 1983), which suggests that food hoarding behaviour may be potentially more prevalent in tropical Asia than has been previously thought. For example, Terborgh (1990) mentioned that little evidence of scatter hoarding had been found in a Bornean forest.

Food hoarding behaviour may allow animals to optimise foraging and feeding, and to improve chances of survival during food scarcity. The former factor appears more effective on a short time-scale, while the latter factor seems rather important on a longer time-scale.

Fruit production in tropical rain forests fluctuates substantially within and between years both in Southeast Asia (Medway 1972, Leighton & Leighton 1983, Whitmore 1984, Yap & Chan 1990, Yasuda 1998) and other tropical regions (Smythe 1970, Sourd & Gautier-Hion 1986, Foster 1996). Such seasonal fluctuations in food availability have been suggested as a factor in the evolution of food hoarding behaviour (Smith & Reichman 1984, Vander Wall 1990). Forget (1996) showed that the seasonal hoarding behaviour of rodents in French Guiana was associated with the fruiting seasonality. In addition, Kanzaki *et al.* (1997) studied the survival and germination of buried seeds packed in aluminium mesh bags in a Malaysian tropical rain forest and found that a proportion (16%) of primary forest species remained viable in soil exceeding one year. This implies that certain seeds could be hoarded as provisions for the period of food scarcity even in tropical rain forests.

Food hoarding behaviour of *Leopoldamys sabanus* differed significantly from that of *Lariscus insignis* (Table 1). The former tended to store fruits on the ground, usually covered with leaves, while the latter primarily hoarded fruits in soil, which is the typical scatter hoarding among rodents (Vander Wall 1990). The two species are nocturnal and diurnal respectively. Smith and Reichman (1984) suggested that hoarding behaviour serves to optimise foraging with regard to competitors. Other species with different activity patterns from the hoarding species may be more critical cache robbers than conspecifics, because the hoarder cannot protect its caches against the former when it is inactive. The difference in hoarding behaviour between *Leopoldamys sabanus* and *Lariscus insignis* might be the result of competition between them. Therefore, we considered that optimising one's foraging through hoarding behaviour is more essential in this case.

In this study, caches were retrieved within a few days after establishment, probably because oil palm fruit is rich in nutrient. Caches containing wild fruits may be retained longer. Forget (1993) suggested that the presence of an alternative food source may reduce the retrieval rate of caches. Therefore, the longevity of caches is expected to be greater during the fruiting season in the region in August–October (Medway 1972), though the present study was carried out in a non-fruiting season.

Food hoarders are effective dispersal agents of plants when they leave, forget, or lose buried seeds (Howe & Westley 1988, Vander Wall 1990, Forget 1993). The maximum distances between the feeding platform and caches observed in this study were similar to those observed in cavimorph rodents in French Guiana

(Forget 1990) but much shorter as compared to those in agoutis in Costa Rica (Hallwachs 1986). Therefore, in spite of the rapid consumption of the caches in the present study, the terrestrial rodents that showed food hoarding behaviour may play an important role as seed dispersers in Malaysian tropical rain forests, though they are known as considerable seed predators (Harrison 1961, Lim 1970, Langham 1983).

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