Effect of food quality and availability on rainforest rodents of Sri Lanka

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Abstract: Tropical rodent communities are highly diverse species assemblages, yet remain poorly studied. This investigation was conducted with the objective of examining the responses of rainforest rodents to food quality and availability. These factors were assessed through laboratory and field trials conducted in the Sinharaja and Kanneliya rainforests in Sri Lanka. The effect of food quality on the foraging behavior of rodents was examined through feeding experiments using natural rainforest fruits/seeds. In addition, the effect of food augmentation on the rodent population was also investigated. Diet choice experiments showed that rodents exhibited clear food preferences, with certain fruit types being preferentially consumed and others rejected. Tolerance tests where animals were provided with a single fruit type showed that some items that were avoided when offered with a range of food items were consumed when no alternatives were available. In the field a positive relationship was found between fruit/seed and rodent densities; seed addition resulted in marked increases in rodent numbers. These results suggest that tropical rodent populations are food limited, at least during seasons when fruits/seeds are in short supply. Food selectivity also means that populations of rainforest rodents might be adversely affected by changes in tree species composition resulting from habitat disturbance and fragmentation.

Keywords: Fruits, rainforest, rodents, seed predation, Sri Lanka

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INTRODUCTION

Seeds and fruits are key food resources of many animals, especially ants, birds and small mammals (Kelt et al. 2004). Through their feeding habits small mammals such as rodents promote seed dispersal by hoarding seeds (Wall 2001), and they influence the structure and composition of plant communities via seed and seedling predation (Alcantara et al. 2000; Kelt et al. 2004; Hoshizaki & Miguchi 2005). The availability of food resources is one of the most important factors that govern animal populations. In temperate environments, where food supplies are seasonal, animal population fluctuations are said to be primarily driven by food (Dunning & Brown 1982; Clifford & Anderson 2001). In tropical rainforest systems, because of higher plant species richness and lower degree of seasonal variation, one would expect animals to have an abundant food supply at all times. However, in consuming food resources, animals exhibit preferences in terms of quality and availability. The optimal foraging theory (MacArthur & Pianka 1966) predicts that when faced with food types of varying quality with respect to their palatability (e.g. the presence of toxic compounds) and nutritional value, a forager will select the food types with highest energetic returns in preference to others (Pyke et al. 1977; Krebs 1978). The potential value of a food item is also determined by its search and handling times. A food item that requires greater handling time may be less profitable in terms of the net energy gained by consuming it. In tropical environments rodents may also face food shortages during certain periods of the year, when their foraging decisions become crucial. Many researchers have speculated that food limitation is responsible for the fluctuation of rodent populations in rainforest habitats (e.g. Alder 1994; Dunstan & Fox 1996; Shanker & Sukumar 1999; Wijesinghe 2006), although no study has experimentally manipulated food type and quantity to test this hypothesis in rainforests of South and Southeast Asia.

In complex and biodiversity-rich tropical forest ecosystems, assessing the extent of food selectivity exhibited by rodents and their response to food availability would be useful to predict their influence on the structure and composition of plant communities. Such information will also be important to ascertain potential impacts of forest disturbance on small mammals, and to provide insight into the patchy distribution of small mammal assemblages. This paper reports the results of two investigations. First, it studies the diet selection of three rodents, and second it tests the response of rodent populations to food availability in a tropical rainforest ecosystem. With regard to the first study of diet selection, we hypothesized that an individual forager when offered a range of food items, its choice of a food item should represent its preferred food resource. But when the range of food items is limited, it should forage on the less preferred food items. In the second study on food availability we predicted that in populations that are limited by food, food enrichment should increase the abundance of that species at the

augmented sites. This study is important for two main reasons: (a) to provide us with information about the diets of a poorly known system, and (b) to allow us to test if tropical forest rodent communities are food limited.

METHODS

The investigations were carried out in two rainforests in Sri Lanka, the Sinharaja and the Kanneliya reserves. The natural vegetation of Kanneliya and Sinharaja is classified as the wet evergreen forest type, which is a climax forest formation. The annual rainfall of the forests ranges from 3750 to 5000 mm and the mean monthly temperature ranges from 18 to 27°C. Much of the precipitation is from the southwest monsoon from May to September and the northeast monsoon from November to January. Endemism among the flora in the forests is particularly high. The forests have a characteristic multistoried structure and a high diversity of species, the dipterocarps being the dominant floral species (IUCN 1993; IUCN & Forest Department 1996).

Study species

Srilankamys ohiensis (The Ceylon Bi-coloured Rat): Phillips (1980), who described this species in 1929, closely allied it to *Rattus niviventer* of the Himalayas. Ellerman (1947) included it as a member of the subgenus *Apomys*, of the genus *Rattus*, because its skull characteristics were thought to resemble those of the *Rattus* species. Subsequently, after many taxonomic considerations, it was seen to differ substantially from all other forms of described Asian murids in its very peculiar cranial features, skin and teeth. Hence Musser (1981) placed it in a separate, monotypic genus *Srilankamys* which is endemic to Sri Lanka. Musser (1981) considered this species to be a relict form, because it possesses a number of primitive characteristics, and speculated that it is possibly related to the stock from which other Indo-Malayan rat-like genera evolved. *S. ohiensis* is a ground dwelling murid confined to the undisturbed rainforests in the island, being more common in the mountainous areas than in lowland regions. *S. ohiensis* has been currently listed as a nationally threatened species (IUCN 2007). Average body weights of male and female *S. ohiensis* are 126±5.3 g and 125±4.3 g respectively.

Rattus rattus kelaarti (The Ceylon Highland Rat) and *R. r. kandianus* (The Common Ceylon House Rat): The species *Rattus rattus* has an extensive distribution. Although native to the Indian Peninsula, it has managed, with humans as the dispersal agent, to colonize all six continents and thousands of islands, invading a variety of habitats from tropical rainforests to arid ecosystems. Consequently, this species shows immense morphological variation. In Southeast Asia it has been conventionally divided into many subspecies. Five subspecies are identified in Sri Lanka, among them *R. r. kelaarti* and *R. r. kandianus* are peculiar to the island while others are introduced. *R. r. kandianus* (average weight male = 133±4.4 g and female = 125±4.1 g) is a commensal of man, being wide spread in the low country and lower hill zones, while *R. r. kelaarti* (average weight male = 130±6.6 g and female =123±7.0 g) is confined to the lowland and montane zone forests in the island (Phillips 1980). Both these species are ground dwelling murids.

Mus mayori (The Spiny Rat): This is an endemic ground dwelling species that is restricted to the moist rainforests of the lowlands and the hill country. *Mus mayori* has been placed in the sub genus *Coelomys*; this species is believed to be a relict form (Crusz 1986). It is represented in the island by two well marked subspecies: the highland (*M. m. mayori*) and the lowland (*M. m. pococki*) forms (Phillips 1980). *M. mayori* has been currently listed as a nationally threatened species (IUCN 2007). Average weights of male and female *M. mayori* are 41±0.66 g and 39±0.6 g respectively.

Investigating food selectivity

The food habits of the rainforest rodents were examined using two methods. The cafeteria experiments were used to investigate food selectivity, and prolonged feeding trials with individual fruit types were used to assess tolerance levels, both of which would indicate differences in quality of food items. These experiments were carried out on three rat taxa, the endemic *Srilankamys ohiensis*, *Rattus rattus kelaarti* and *R. r. kandianus* captured from within the Sinharaja rainforest in 2000 and 2001. These are the three predominant rat species found in this forest. Comparing food habits of these species would reveal information about food preference since these rats are of similar size and hence have similar energy requirements. For instance, the mean weights of females of *S. ohiensis*, *R. r. kelarti and R. r. kandianus* captured from the forest were between 125-123 g. In rainforest habitats these species are predominantly fruigivorous, but *R. r. kandianus* in particular may feed on insects.

Two captive experiments were designed to test the food preference and food tolerance of the three species of rats. The first set of tests, the cafeteria experiments, provided information on the food preferences while the second set, which involved four-day feeding trials using selected food items, provided information on the degree of food tolerance of each species. The feeding experiments were conducted in cages made of wire mesh with wooden frames of size 1 x 0.3 x 0.3 m.

Fruits of 25 tree species from the floor of the Sinharaja forest were used for the food preference tests (Table 1). The months during which the experiments were conducted coincided with the flowering and fruiting seasons of many of the forest tree species. The selection of the fruit types for the feeding trials was based on availability.

Before commencing trials, preliminary tests were carried out to obtain information on handling time of the wild caught rodents. Time spent on handling and ingestion of a food item by each rat was recorded by offering a single fruit and observing the animal for a period of two hours. A given fruit type was tested only once on a selected individual. In the cafeteria experiments, fruits from 25 tree species, 24 from the forest and one from forest areas around the periphery of the reserve were used. Because of the difficulty of simultaneously obtaining all 25 fruit types tested, ten fruit types were presented at a time (two fruits of each type) to each individual rodent, and recordings made of whether the fruits were eaten either fully, partially, or shunned. Additionally, the animals were observed to ascertain which item was selected first from among the given fruits. The experiment commenced on the night subsequent to the night of capture. Trials were conducted at night as this was the active period of the rodents. The experiments commenced at 1900 hr and the results were obtained the following morning at 0700 hr. Each fruit type was tested on 15-20 individuals of both sexes from the three rat taxa. A

given fruit type was tested on an equal number of animals of each taxon. However, because of restrictions in availability the number of animals tested per seed/fruit type varied from 15 to 20. For instance, when fruits were less abundant only 15 animals of each taxon were tested on that particular item, while 20 animals were tested if fruits were highly abundant.

For food tolerance trials, captive rats were tested for their ability to maintain weight over three days on a diet of fruit supplied in excess, one fruit type at a time. Each animal was provided with 100g of a particular fruit type, with water provided ad libitum. The weight of the animal was recorded to the nearest 0.5g using a Pesola balance before and after the experiment. The uneaten fruits were removed from the cage and a fresh supply was provided to the animals on each successive day. Five individuals from each rat taxon were tested on a given fruit type.

Assessing the effect of food availability

The effect of availability of preferred fruit/seed types was assessed by estimating their natural availability and rodent abundance in selected areas of the forest, and through seed enrichment trials. The fruit/seed estimations and the augmentation experiments were conducted in the Kanneliya rainforest during October to February (year 2006 and 2007) which is outside the main fruiting season. The sequence of the study was as follows: a four day trapping, followed by fruit/seed counts, food addition on the same day after the seed/fruit count, and finally another four day trapping session after two weeks.

Six plots of 40x90 m were randomly selected. Live trapping of small mammals was conducted using 50 Sherman's traps per plot, laid in a grid configuration with 10m spacing between each trap. Trapping was conducted for four consecutive nights, yielding a total of 1200 trap nights. Fruit/seed searches were conducted within 2x2 m quadrates by clearing the litter to a depth of about 3cm. Five such quadrates placed at the four corners and middle of each study plot was examined for fruits/seeds consumed in the cafeteria experiments. These were categorized by species and the density of each was calculated.

The influence of food abundance on rodent populations outside the main fruiting season, when food resources could be a limiting factor, was examined through seed enrichment experiments. Seed enrichment was carried out in each of the six study plots. Preliminary investigations revealed that rodents eagerly fed on peanuts, which were therefore selected for the food enrichment trials. Five trays of 20x30x1 cm size, each containing 500g of peanuts were placed on the ground at the four corners and middle of each plot, and they were replenished after a week. After two consecutive weeks of seed enrichment a second trapping session was conducted.

Further confirmation of seed predation by the rodents was sought by using specially designed food trays (Image 1). To allow seed predation by rodents while preventing the activity of ants and birds, the method of Herrera et al. (1994) and Alcantara et al. (2000) were used with a few modifications. The peanuts were pasted using ant proof glue on the tray, evenly spread in a grid fashion. Pasting the seeds in this manner prevented the removal of seeds by ants. The entire tray was then covered by a mesh box to prevent seed predation by birds. Openings of 10x25 cm on the two sides of the mesh box allowed free access to rodents but prevented entry of large

Image 1. Specially designed food tray used for confirmation of seed predation by the rodents

granivores. At the entry point leaf litter was piled so that the entrance was not obvious. The mesh box was also covered by a hard, non-transparent polythene sheet to prevent rainwater seeping into the tray and to be less visible to the birds. Faecal matter found on food trays was identified and used as evidence for the presence of rodents.

RESULTS

Food selectivity

The diet choice experiments showed that rodents exhibited food selectivity, in that some fruits were eaten fully while others were avoided without being consumed. From among the seeds provided, certain seed types were preferred whilst others were not consumed (Table 1). Observations revealed that all three rat taxa selected *Elaeocarpus glandulifer*, *Syzygium rubicundum* and *Clidemia hirta* as their first choices in the fruit combinations provided. Items avoided included *Chaetocarpus castanocarpus*, *Mussaenda frondosa*, *Calamus ovoideus*, *Fagrea ceilanica* and *Semecarpus moonii*.

Chi-square test of independence was used to ascertain if the responses of a given taxon for a particular seed type showed significant variations (Table 1). The number of responses for each category, i.e., for fully eaten, partially eaten and not eaten, was used for this purpose. For the majority of the fruit types, the responses of the rat taxa were either identical or not statistically different from each other. Contrasting responses were evident for only four of the 25 fruit types. The results thus showed that rodents differed significantly in their preference for the fruits of *Doona congestiflora*, *Syzygium neesianum*, *Gomphia serrata* and *Melastoma malabathricum* (Table 1). While *Chaetocarpus castanocarpus*, *Calamus ovoideus*, *Mussaenda frondosa*, *Fagrea ceilanica* and *Semecarpus moonii* were completely rejected by all three rodents, the fruits of *Syzygium rubicundum* and *Clidemia hirta* were fully eaten by all taxa (Table 1).

A two way ANOVA was used to test if handling times differed significantly between the rodents and seed type. Seed type, rodent species and their interactions were the independent variables (factors), while handling time was the dependent variable. The results revealed that handling time significantly differed between seed types ($F_{22}=55.97$, P=0.0001). However,

Table 1. Selection of 25 different fruit types by three rodents *Srilankamys ohiensis*, *Rattus rattus kelaarti* and *R. r. kandianus* during cafeteria trials. The responses of the rodents were scored as fully eaten (Ful.), partially eaten (Par.) or not eaten (Not). Probability values are from chi-square tests of independence.

Plant species	S. ohiensis			R. r. kelaarti			R. r. kandianus			
	Ful.	Par.	Not	Ful.	Par.	Not	Ful.	Par.	Not	P
# *Doona congestiflora*	4	10	1	12	2	1	10	3	2	0.017*
# *D. affinis*	8	7	0	12	3	0	11	4	0	0.260
# *D. trapezifolia*	15	5	0	12	8	0	18	2	0	0.091
Timonius jambosella	13	7	0	15	5	0	15	5	0	0.720
Elaeocarpus serratus	7	8	0	4	11	0	10	5	0	0.090
E. subvillosus	0	7	8	0	11	4	0	9	6	0.329
E. glandulifer	14	1	0	14	1	0	13	2	0	0.760
# *Aporusa cardiosperma*	0	15	0	3	12	0	4	11	0	0.111
# *A. lanceolata*	0	13	2	3	10	2	0	13	2	0.165
Coscinium fenestratum	9	6	0	8	5	2	7	6	2	0.668
Chaetocarpus castanocarpus	0	0	20	0	20	0	0	0	20	SR
Syzygium rubicundum	15	0	0	15	0	0	15	0	0	SR
# *S. neesianum*	0	0	15	1	13	1	3	7	5	0.001**
# *Calamus ovoideus*	0	0	20	0	0	20	0	0	20	SR
Gomphia serrata	0	0	15	0	0	15	3	4	8	0.002**
Mussaenda frondosa	0	0	15	0	0	15	0	0	15	SR
# *Cullenia ceylanica* $	0	15	0	0	13	2	0	12	3	0.207
Eurya accuminata	0	8	7	1	8	6	3	8	4	0.364
# *Dipterocarpus zeylanicus*	6	9	0	9	6	0	10	5	0	0.310
Myristica dactyloides	0	0	15	0	5	10	0	4	11	0.054
Clidemia hirta	15	0	0	15	0	0	15	0	0	SR
Melastoma malabathricum	0	6	9	0	12	3	3	11	1	0.003**
Fagrea ceilanica	0	0	15	0	0	15	0	0	15	SR
Camellia sinensis	0	8	7	4	8	3	2	10	3	0.149
# *Semecarpus moonii*	0	0	20	0	0	20	0	0	20	SR

* - P<0.05; ** - P<0.01; # - Endemic fruit species; SR - fruit types to which the three rat taxa responded identically.
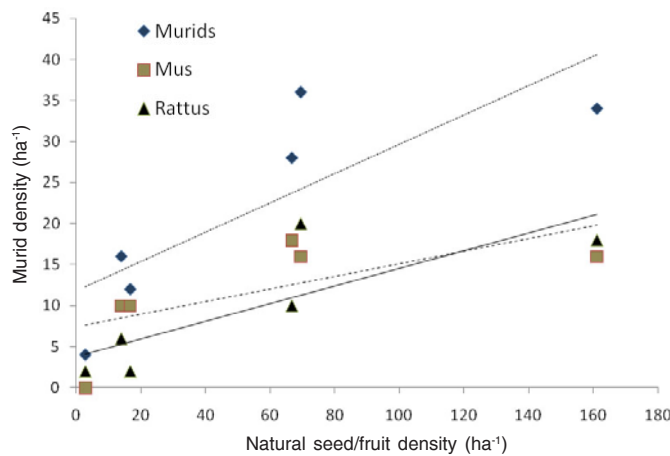

Figure 1. Relationship between seed/fruit density on the forest floor and densities of *M. mayori* (solid squares), *R. r. kandianus* (solid triangles) and total murids (solid diamonds).

Figure 2. Densities of murids in the six study plots in the Kanneliya rainforest before (soild bars) and after (open bars) food addition

there were no differences in handling times between the three rat taxa ($F_2 = 0.59$, P=0.557). The interaction between rat taxa and seed types was also not significant ($F_{44} = 0.45$, P = 0.999) indicating that all 3 rat taxa spent similar times on the various seeds.

The different taxa displayed varying degrees of food tolerance (Table 3). *R. r. kandianus* maintained weight on 15 seed types, *R. r. kelaarti* on 13 and *Srilankamys* on nine. Weight loss occurred with some fruit types that were offered. Both *S. ohiensis* and *R. r. kelaarti* loss weight on 11 fruit types (Table 3). Some items that were avoided during the cafeteria tests were consumed during the food tolerance trials. For example *S.*
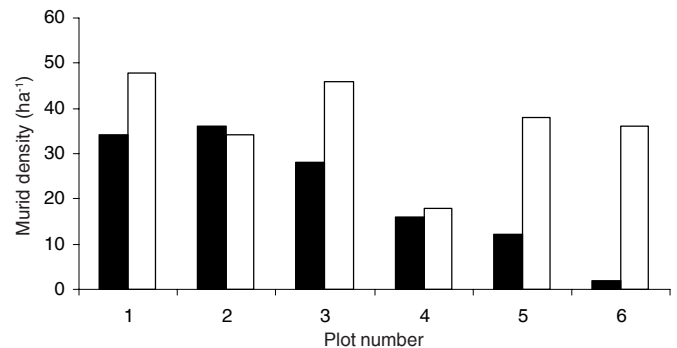
ohiensis did not show any interest in the fruits of *Syzygium neesianum*, *Myristica dactyloides*, *Gomphia serrata* and *Mussaenda frondosa* during cafeteria experiments, but these were ingested when other food types were not available.

Effects of food augmentation

In the trapping sessions in the Kanneliya forest, both before and after food addition, with the exception of one individual of *Suncus zeylanicus* (Sri Lanka Jungle Shrew; Phillips 1928), all the captures were of the two murids *Mus mayori* and *Rattus rattus kandianus*. Prior to food enrichment there was a significant difference in the numbers of rodents captured in each of the six study plots (Chi-square test - $\chi^2 = 20.39$; P = 0.001).

With regard to the link between rodents and fruit/seeds availability, prior to food addition it is seen that over 50% of the variation in the rodent population is explained by fruit/seed densities (Total murids $R^2 = 66.4$ %, F = 7.92, P = 0.04)

Table 2. The mean lengths and weights (n=50) and the mean handling times (± standard deviations) of 25 fruit types collected from areas within and adjacent to the Sinharaja forest. Handling time is the average time (n=5) an animal spent handling and consuming (totally or partially) one fruit within the first two hours of supplying it. The handling times were recorded for the three taxa *Srilankamys ohiensis* (*S. o.*), *Rattus rattus kelaarti* (*R. r. kl.*) and *R. r. kandianus* (*R. r. kd.*) separately. Table show handling times of fruit types that were fully consumed, not fully consumed within two hours (round parentheses), not consumed but nevertheless handled (square parentheses) and neither consumed nor handled (-) are also shown. No standard deviations have been given in instances where only one individual was seen to handle a food item.

Fruit species	Lenth (mm)	Weight (g)	Handling time (mins)		
			S. o.	*R. r. kl*	*R. r. kd*
Seeds fully eaten in 2hrs by all rodents					
Doona congestiflora	8.76±1.17	0.26±0.10	2.45±0.40	2.61± 0.41	2.70±0.65
* *D. affinis*	5.89±11.48	0.19±0.35	3.63±1.78	4.43±0.63	4.18±0.91
* *D. trapezifolia*	12.04±0.88	1.58±0.21	12.84±1.57	12.40±1.89	10.42±1.29
E. glandulifer	18.12±17.39	1.23±0.38	5.10±2.10	6.64±2.01	6.12±1.82
Coscinium fenestratum	20.96±1.67	3.81±0.86	11.45±2.27	11.74±2.35	10.77±2.20
Syzygium rubicundum	7.84±1.06	0.46±0.09	1.81±0.53	1.81±1.34	2.68±1.48
Eurya accuminata	5.12±0.69	0.24±0.02	3.03±1.14	3.07±1.19	3.70±1.53
Clidemia hirta	9.70±0.82	0.29±0.12	2.60±0.70	2.35±0.60	2.73±1.16
Melastoma malabathricum	19.77±3.95	2.97±1.31	13.36±2.24	11.07±2.56	11.50±1.44
Seeds partially eaten within 2hrs by any one or more rodents					
Timonius jambosella	16.84±2.13	1.01±0.30	(8.32)±1.43	(10.03)±1.69	(8.13) ±1.51
Elaeocarpus serratus	27.45±1.81	9.45±0.86	[18.12]±6.70	(20.11)±5.09	(20.70)±3.00
E. subvillosus	31.70±2.88	9.42±1.57	[18.71]±2.70	(18.29)±2.98	(17.53)±2.12
* *Aporusa cardiosperma*	15.22 ±1.75	1.00±0.30	(10.87)±3.31	(9.80)±2.21	(10.30)±2.41
* *A. lanceolata*	9.24±1.31	0.29±0.10	(4.56)±1.59	(4.27)±1.09	(4.03)±0.96
* *S. neesianum*	22.03±2.27	2.80±0.94	[14.80]±1.57	(15.33)±3.07	(15.82)±2.45
Gomphia serrata	9.39±0.86	0.25±0.03	8.84±1.78	(10.06)±2.62	(9.51)±1.56
Cullenia ceylanica	105.06±12.06	102.42±28.34	(31.08)±11.11	(39.79)±10.31	(37.81)±11.79
* *Dipterocarpus zeylanicus*	23.03±3.60	9.83±2.13	(19.77)±2.39	(18.91)±4.67	(18.74)±2.42
Myristica dactyloides	38.70±2.82	23.71±1.49	[20.52]±14.61	(18.27)±7.76	[17.84]±6.95
Seeds not consumed (but handled) all rodents					
Fagrea ceilanica	51.10±4.29	25.16±3.81	[11.15]±6.33	[11.75]±7.74	[13.24]±6.37
Camellia sinensis	17.04±3.39	7.07±2.31	[12.44]±2.44	[14.55]±2.95	[14.80]±1.87
* *Semecarpus moonii*	21.34±6.41	1.63±0.27	[4.25]±3.44	[4.81]±3.35	[4.82]±4.09
Seeds not consumed or handled by all rodents					
Chaetocarpus castanocarpus	11.56±1.75	0.18±0.02	-	-	-

* Endemic fruit species.

under natural conditions (Fig. 1). There were significant differences in fruit/seed densities between the plots (Table 4). The food addition experiments confirmed the favourable impact of food availability on rodent populations (Fig. 2). The patterns observed in each of the individual plots are shown in Fig. 2. Paired t-test results suggest a significant difference in murid density before and after food enrichment (T = 2.73, n=6, P = 0.04). All plots (except plot 2) showed an increase in rodent density (Fig 2) after addition of food. Taking individual plots, the plot that had the lowest original density of 4 x 10^{-4} ha^{-1} increased to 36 x 10^{-4} ha^{-1} after food addition. It is noteworthy that this increase in density was more than double in plot 5 and 6 where the initial densities were low indicating that the effect of resource augmentation was most significant in the resource poor plots.

DISCUSSION

This study has revealed that the abundance and distribution of frugivorous rodents even in resource rich tropical rainforests are greatly influenced by the availability of preferred food types, providing direct evidence for the food limitation hypothesis in these ecosystems. Very few studies have examined food habits of tropical rodents in captivity or under natural conditions. The findings of the present investigation indicate that rainforest rodents actively select certain fruit types from the wide range that is available to them on the forest floor. The study also highlights the fact that the availability of preferred fruits varies throughout a given rainforest, which in turn causes uneven occurrence patterns of the rodents. This observation is of special relevance to the distribution of rodent populations within the Sri Lankan rainforests where many studies have shown that the occurrence of tree species is patchy and highly localized (e.g. Gunatilleke & Gunatilleke 1981; Gunatilleke & Ashton 1987). Although tropical rainforests harbor a multitude of trees that bear seeds and fruits, which presumably provide an abundant source of food throughout the year for frugivores, the present investigation conforms to the hypothesis that rodents actively consume only selected food items based on the ease of handling (Goodyear 1992). Although this was not tested in the present study, observations revealed the trend that the rats mostly consumed fruit types with a fleshy pulp and a thin, easily chewable outer peel.

Aversion to particular plants or parts of plants may result

Table 3. The mean differences in body weights of animals (g) over 24 hours and the mean weights of each fruit type consumed (g) per day per animal (n = 5) ± standard deviations, over a four-day feeding trial involving three selected rat taxa.

Fruit species	S. ohiensis Difference in body weight	S. ohiensis Weight of fruit consumed	R. r. kelaarti Difference in body weight	R. r. kelaarti Weight of fruits consumed	R. r. kandianus Difference in body weight	R. r. kandianus Weight of fruits consumed
* Doona congestiflora	0.27± 0.59	21.40±1.60	0.17±0.41	20.97±3.39	0.03±0.48	21.03±3.63
* D. affinis	0.17±0.62	17.19±3.35	0.17±0.52	17.32±2.81	0.07±0.42	16.07±2.60
* D. trapezifolia	0.60±0.63	21.57±3.60	0.27±0.90	17.70±3.22	0.30±0.70	17.00±3.77
Timonius jambosella	(0.30)±0.86	14.63±4.36	0.17±0.49	14.72±5.21	0.27±0.53	11.98±5.61
Elaeocarpus serratus	0.07±1.03	15.06±4.82	0.23±1.32	16.53+4.40	0.27±0.63	18.69±2.90
E. subvillosus	(1.10)§±0.54	7.87±4.73	(0.07) §±1.05	9.76±3.43	(0.23)±0.82	10.05±3.85
E. glandulifer	0.53±0.79	20.59±5.57	0.30±0.90	17.05±5.34	0.27±0.68	18.70±4.93
* Aporusa cardiosperma	0.33±0.85	18.70±2.48	0.20±0.53	15.38±3.28	0.04±0.45	20.22±4.47
* A. lanceolata	(0.17)±0.67	17.58±2.67	(0.10)±0.60	12.95±3.90	0.13±0.97	15.67±3.32
Coscinium fenestratum	(0.10)±0.89	16.99±4.45	0.03±0.64	19.17±4.19	0.03±0.61	17.44±4.61
Chaetocarpus castanocarpus	(1.80)§±0.57	-	(1.00) §±0.55	-	(1.80) §±0.57	-
Syzygium rubicundum	0.43±0.70	19.59±7.11	0.70±1.00	18.08±5.86	0.20±0.56	16.04 ±3.93
* S. neesianum	(0.35)±0.95	14.67±2.49	0.20±0.94	17.45±5.59	0.43±0.86	16.89±3.15
* Calamus ovoideus	(2.00)§±0.61	-	(1.70)§±0.67	-	(1.80) § ±0.57	-
Gomphia serrata	(1.80)§±0.57	4.141±0.29	(0.90) §±0.42	3.99±0.45	(1.00) §±0.61	4.72±1.97
Mussaenda frondosa	(1.58)§+0.92	4.53±1.30	(0.56) §±0.98	7.08±3.80	(1.21) §±(0.81)	6.14±3.23
* Cullenia ceylanica	0.03±0.92	13.93±3.00	(0.13)±0.74	14.98±3.86	0.07±0.86	16.62±1.91
Eurya accuminata	(0.92)§±0.49	4.89±2.95	(0.18) §±0.67	8.04±3.51	0.11±0.56	10.20±3.41
* Dipterocarpus zeylanicus	0.23±0.53	21.38±3.88	0.03±0.40	19.95±3.14	0.20±0.46	19.90±2.69
Myristica dactyloides	(1.50)§±0.61	3.14 ±1.10	(1.70) §±0.67	3.67±0.93	(1.60) §±0.42	3.53 ±1.14
Clidemia hirta	(0.23)±0.82	15.83±2.94	0.23±1.08	17.50±2.94	0.67±0.70	17.55±4.75
Melastoma malabathricum	(0.80)§±0.48	7.62±3.02	(0.29) §±0.60	7.94±2.54	(0.60) §±0.39	9.58±4.31
Fagrea ceilanica	(1.80)§±0.57	1.30	(1.80) §±0.27	0.31	(1.60) §±0.82	2.8
Camellia sinensis	(0.94)§±1.26	16.61±5.62	(0.61) §±0.63	15.48±5.30	(0.07)±0.47	12.38±4.59
* Semecarpus moonii	(1.90)§±0.42	-	(1.90) §±0.22	-	(1.60) §±0.82	-

* Endemic fruit species; § Instances where total or partial starvation or death of an animal was evident. Weight losses are shown in parentheses.

from olfactory and gustatory responses, spines, hard shell, dense husks, or other structural features (Randolph et al. 1991). It may also be a reaction to an unpleasant taste resulting from noxious or toxic secondary compounds (Freeland & Janzen 1974; Bryant & Kuropat 1980). In Brazil, Bergallo & Magnusson (1999) have shown that terrestrial small mammals such as small forest dwelling rodents, in particular, select fruits and seeds that have a high energy content and nutritional value, whilst avoiding those containing toxic compounds. In the present study rodents were low in areas that had *Chaetocarpus castanocarpus* which has a spiny outer covering.

Numerous examples from captive experiments and field studies in temperate countries have demonstrated that, as the supply of the more preferred food item declines, a species becomes less selective (e.g. Krebs et al. 1977; Sinclair et al. 1982). The present investigation suggests that such a phenomenon may also occur in tropical rainforest ecosystems. In the feeding trials with selected fruit types, when preferred alternatives were not available, all three rat taxa fed on fruit types that they refrained from consuming during the cafeteria trials. In situations when food is scarce, if the animal continued to refrain from feeding owing to the absence of preferred food items it would lose weight even faster than if it fed on lower quality food items, and this in turn would reduce the time the animal can withstand nutritional stress before dying. Therefore, despite the loss in weight, it is profitable for animals to consume fair quantities of even the low quality food items.

In New Zealand, a temperate country, Choquenot & Ruscoe (2000) attributed the sporadic eruptions in rodents to an increase

in food availability. Similar observations have been made by Angelstam et al. (1987). In the present study a positive correlation was evident between rodent densities and the availability of palatable fruits/seeds in the rainforest. The food enrichment trials provided further evidence that the availability of favourable resources is positively linked to increases in rodent populations. Both rodent species, *M. mayori* and *R. r. kandianus*, increased in abundance in all plots except in plot 2, with seed addition. It was particularly noteworthy that the increase in abundance was of a much higher magnitude (more than double) in the previously sparsely populated plots than in others. Boutin (1989) reviewing 138 cases that have used food enrichment experiments under field conditions to investigate its impact on animal populations have concluded that there has been 2-3 fold increases in densities in response to food supplementation. However, as pointed out by this reviewer, it would be preferable to use long term experiments conducted over a large special scale in order to draw firm conclusions. The findings of the present investigation nevertheless provide some evidence for the food limitation hypothesis in tropical rainforest ecosystems. Although Sri Lanka's wet zone has been described as aseasonal (Ashton & Gunatilleke 1987) the forest has distinct periods of flowering and fruiting. The main fruiting season in lowland wet zone forests is during the months of April to August when rainfall is heavy. Increased populations occur at this time, presumably because food is more abundant (Leung 1999; Wijesinghe 2006).

For predominantly frugivorous rainforest species, the

Table 4. Density of seeds/fruits found on the floor of each of the six plots in the Kanneliya rainforest.

Study Plot	Tree species	Seed/fruit density (ha⁻¹)
1	*Coscinium fenestratum*	5.56
	Elaeocarpus subvillosus	27.78
	Timonius jambosella	16.67
	Semecarpus moonii	5.56
	Aporusa lanceolata	19.44
	Cullenia ceylanica	22.22
	Palaquium thwaitesii	8.33
	Myristica dactyloides	11.11
	Myristica fragrans	5.56
	Palaquium grande	44.44
2	*Palaquium thwaitesii*	2.78
	Bhesa ceylanica	44.44
	Stemonoporus kanneliyensis	13.89
	Dillenia retusa	8.33
3	*Palaquium grande*	2.78
	Dillenia suffruticosa	22.22
	Cullenia ceylanica	13.88
	Bhesa ceylanica	27.78
4	*Chaetocarpus castanocarpus*	136.11
	Dillenia retusa	5.56
	Cullenia ceylanica	8.33
5	*Cullenia ceylanica*	16.67
6	*Cullenia ceylanica*	2.78

scarcity of good quality food would be particularly important outside the main fruiting season. Consequently, during such food shortages, animals could be expected to aggregate in selected seed-rich areas where the preferred food types are available. The findings of this study also imply that frugivorous rodents could be adversely affected if the tree species composition of these ecosystems is altered through habitat disturbance and fragmentation.

CONCLUSION

Food availability, particularly during the non-fruiting season, may at least in part be responsible for the regulation of rodent populations in tropical rainforests. The study also shows that the scarcity of food during the non-fruiting season may be aggravated due to the food selectivity exhibited by these rodents.

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