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# Foraging Patterns of Black Rats across a Desert-Montane Forest Gradient in the Galápagos Islands

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## ABSTRACT

The cosmopolitan black rat (*Rattus rattus*) has been introduced to several islands of the Galápagos Archipelago, Ecuador, where it has become established in all vegetated habitats. The foraging behavior of this ecologically versatile species was studied through detailed analysis of stomach contents of rats trapped in four very different Galápagos habitats: thorn scrub, savanna, montane scrub, and montane forest. Plant foods comprised an average of 80 percent of stomach contents; however, animal food occurred in at least 81 percent of the rats in each population, and *R. rattus* reproduction was correlated with a high level of animal food in the diet. Although the rats fed on an extremely broad range of plant and animal foods, they were very selective feeders, discriminating among plant species and among parts of plants. Fruits and seeds were preferred foods, and in most cases the seeds were destroyed. These introduced rodents are probably having many severe effects on the Galápagos flora and fauna.

## RESUMEN

La cosmopolita "rata negra" (*Rattus rattus*) ha sido introducida a varias de las Islas Galápagos, Ecuador, donde se ha establecido en todos los habitats con vegetación. El comportamiento alimenticio de esta ecológicamente versátil especie se estudió por medio del análisis detallado del contenido del estómago de ratas atrapadas en cuatro habitats distintos de Galápagos: maleza árida, sabana, maleza húmeda, y bosque húmeda. Alimentos vegetales comprendieron un promedio de 80% del contenido de los estómagos; no obstante, alimentos de origen animal ocurrieron en por lo menos 81% de las ratas de cada población, y hubo una correlación entre la reproducción de *R. rattus* y un nivel elevado de alimento animal en la dieta. Aunque las ratas comieron una ranga muy amplia de alimentos, seleccionaron cuidadosamente su comida. Discriminaron entre especies de plantas y entre las partes de las plantas. Prefirieron frutas y semillas, y destruyeron la mayoría de las semillas. Es probable que estos roedores introducidos causen muchos daños a la flora y fauna de Galápagos.

THE BLACK RAT, *Rattus rattus* L., is a highly successful, cosmopolitan tramp species. In many parts of the world (particularly in the tropics and subtropics), it has invaded an extremely wide range of environments (Strecker and Jackson 1962, Kami 1966, Best 1969, Fall *et al.* 1971, Tigner 1972). In the Galápagos Archipelago, Ecuador, this species has become established on six major islands and several islets, where it now occupies all available vegetated habitats, from desert scrub to lush montane forest.

Prior to the arrival of *R. rattus* in Galápagos, the islands supported six endemic species of rice rats (*Oryzomys* and *Nesoryzomys* spp.). On all islands that have been reached by the black rat, however, the endemic rats have subsequently disappeared (Brosset 1963). Thus, wherever they now occur in Galápagos, black rats are the only rat-sized rodents present (in some habitats they do coexist with the much smaller, introduced house mouse, *Mus musculus* L.).

The ecological plasticity of this extremely successful colonizer necessarily involves the ability to obtain an adequate diet in a wide variety of environments. Analysis of the foraging patterns of *Rattus rattus* can therefore provide insight into this species' success. The Galápagos Islands are an espec-

ially suitable setting for such analysis because of the wide spectrum of habitats currently occupied by black rats, and the absence of close competitors. Additional interest derives from the fact that approximately one-third of the vascular plant taxa in Galápagos are endemic (Wiggins and Porter 1971), and are thus completely new to these introduced rodents.

From 1973 to 1976 I studied the feeding ecology of black rats in a broad range of Galápagos habitats. Analyses of intra-population diet differences and of patterns of diet breadth and sampling are presented elsewhere (D. A. Clark 1978, 1980). In this paper I describe the composition of diets selected by black rat populations over the Galápagos habitat spectrum, and I analyze the relationships among diet composition, available foods, and reproduction.

## METHODS

I collected and preserved in 95 percent ethanol the stomachs from all or most individuals trapped from each of eight black rat populations in the Galápagos Islands. The animals were snap-trapped in four permanent 5.1 ha grids (256) traps, 15 m spacing, located in distinct habitats (fig. 1): (1) lush montane forest (Santa Cruz Island) dominated by the endemic composite tree, *Scalesia pedunculata*, and with a dense

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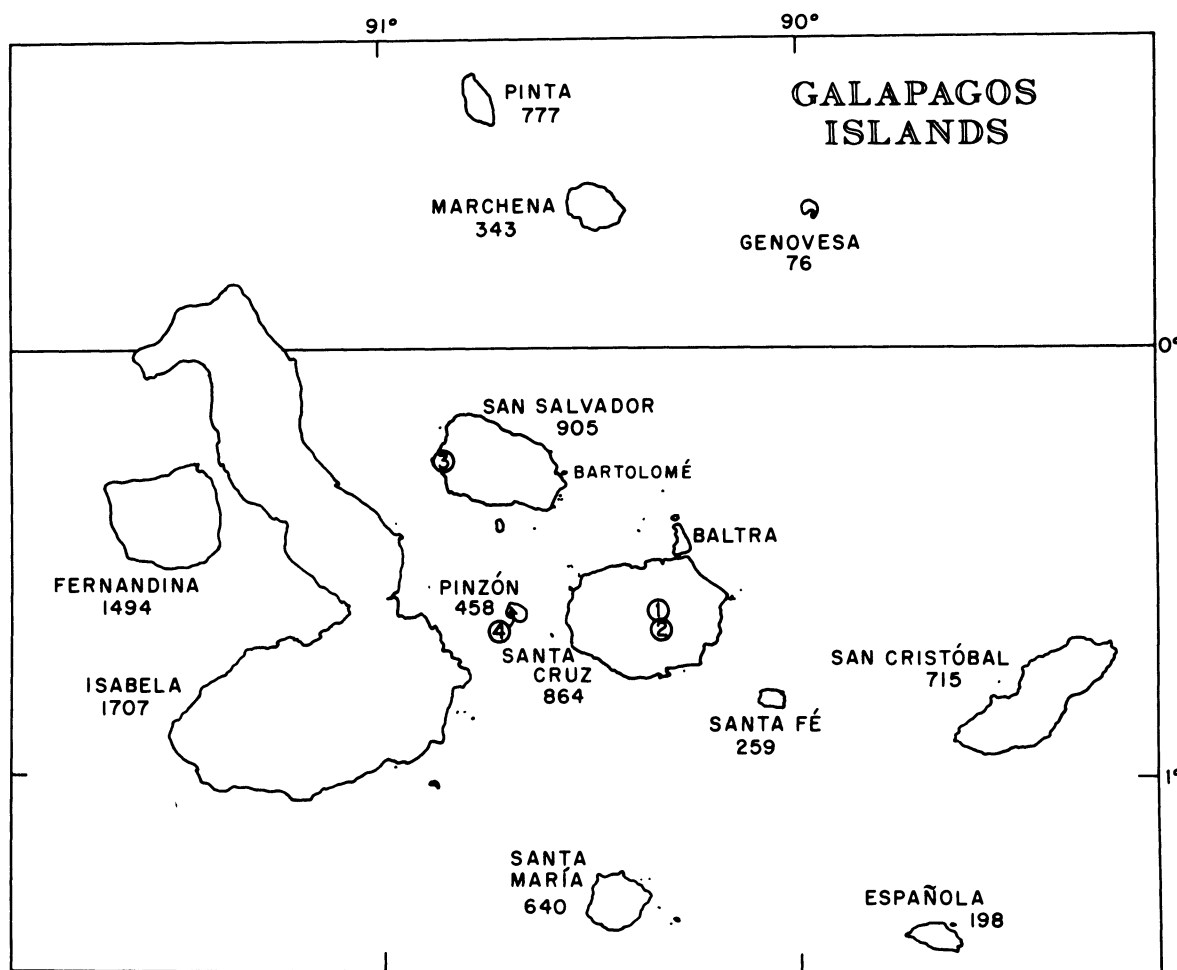


FIGURE 1. Location of the four study sites in the Galápagos Islands, Ecuador. (1) montane forest; (2) montane scrub; (3) savannah; (4) thorn scrub. Altitudes (m) of the major islands are indicated.

understory; (2) montane scrub (Santa Cruz Island) dominated by the endemic shrub, *Miconia robinsoniana*, and ferns; (3) open savannah (San Salvador (=Santiago) Island) dominated by *Bursera graveolens* trees and shrubs; and (4) thorn scrub (Pinzón Island) an arid rocky habitat with low trees and shrubs. Each rat population sample was collected by trapping the grid on consecutive nights until residents were removed (D. B. Clark 1980). For each grid one population sample was collected during the "hot" season (January-May) and another during the "garúa" season (June-December). The seasonal climate and vegetation of these habitats are described in detail in D. B. Clark (1980). For all animals, standard autopsy data (body measurements, weight, sex, and reproductive condition) were recorded.

The contents of each stomach from the 1973

montane scrub population were emptied into a Petri dish and examined under a dissecting microscope. For all other samples, stomach contents were emptied into a dish filled with alcohol; this procedure prevented the materials from drying out and losing their distinguishing characteristics, and it also made possible a thorough examination of the contents.

Stomach contents were analyzed in detail (an average of 3-4 hours of microscope work per stomach). Using a reference collection of plant materials, I identified all plant foods as precisely as possible (i.e., exact part of plant as well as species or genus); I used microscopic characters, such as epidermal pattern, trichomes, cellular inclusions, and starch grains, as well as shape, texture, and color of particles. Animal foods were identified to phylum or class, and the presence of a few distinctive arthropod species

was noted. After separation of the foods in each stomach, I recorded all food types present and visually estimated the percent volume represented by each (bait was excluded from these estimates). Unidentified material rarely comprised more than 10 percent of the stomach contents. Stomachs with less than 0.25 g contents were excluded from quantitative analyses, to avoid biases from nearly empty stomachs. I also excluded animals which had eaten rats or mice (they were trapped on nights when partially eaten rodents were found in traps). Because of marked temporal changes in food availability, I compare only animals caught within the first 3-6 days of trapping.

For the analyses presented in this paper I include only adult-sized rats ( $\geq 136$  mm body length), to avoid the complicating factor of ontogenetic dietary changes (D. A. Clark 1980). The few instances of dietary differences between males and females are detailed in D. A. Clark (1980); for the present analyses, the sexes are treated together.

During all trappings except the first (montane scrub, 1973), I assessed the abundance of certain food types in 0.25 m<sup>2</sup> quadrats located randomly over the trapping grid (N = 100, 1976 montane forest and 1975 montane scrub; otherwise N = 50). In all quadrats I identified and counted all seeds and fruits. Large, sedentary invertebrates were also counted. Plant species with leaves were recorded for 1975 and 1976 quadrats.

Samples of important foods were collected from the grid sites for nutritional analysis. The samples were oven-dried at 60°C, finely ground with a mortar and pestle, and subjected to a complete proximate analysis (A.O.A.C., 1975) and elemental analysis (by emission spectrophotometry) at the WARF Institute, Madison, Wisconsin.

Statistical tests referred to in this paper are taken from Siegel (1956).

## RESULTS

**OVER-ALL DIET COMPOSITION.**—The data presented in the appendix summarize the diet of adult *Rattus rattus* trapped in the four study sites in each of the two seasons. In all cases the rats were true omnivores, i.e., they fed on a combination of plant and animal foods. Plant materials (including fungi) predominated, comprising an average of 80 percent (43-99%) of the volume of the diet of each population.

An extremely wide variety of foods was eaten, including seeds, fruits, leaves, buds, flowers, herbaceous and woody stems, starchy roots and rhizomes, a variety of fungi, lichens, many kinds of insects, other invertebrates (centipedes, snails, and earth-

worms), and some vertebrate material. Arthropods, seeds, and fruits were included in the diet of all populations. As many as 22 species of vascular plants occurred in the diet of a single population.

**SELECTIVITY IN FEEDING.**—Even though their diet is very broad, Galápagos black rats are highly selective feeders. The study populations used an average of only 32 percent (17-61%) of the vascular plant species present in the habitat. They also selected only specific parts of the plants included in the diet, and the parts selected varied among species. An example is the usage of *Prosopis juliflora*, a dominant plant of the thorn scrub site. In the dry (garúa) season, *Prosopis* leaves comprise a large proportion of the green matter available (and contain 24 percent crude protein on a dry-weight basis); however, this potential food was virtually untouched by the dry-season sample of rats (1 of 38 rats had eaten a trace amount). In contrast, *Prosopis* seeds and buds occurred in many rat stomachs, and middens of gnawed young *Prosopis* stems were scattered through the grid (wood fibers were an important constituent of the stomach contents). Although *Prosopis* leaves were rejected, I identified leaves of a total of 24 plant species in the stomachs from the eight population samples (this total excludes the distinctive, secondarily ingested leaf material from the gut of insect prey).

In most cases, however, the rats rejected leaves and stem and preferentially ate the reproductive parts of plants. In the 1975 savannah population, for example, 80 percent of the sampled rats had eaten flowers or fruit of the vine, *Passiflora suberosa*, but none had eaten the (much more abundant) leaves (appendix 1). The fruit was the only regularly eaten part of several species, and for many other plants, only the seeds were found in stomach samples (appendix 1).

The rats' preferential feeding is further illustrated by their disproportionate usage of uncommon foods. While *Passiflora suberosa* fruits and flowers had been eaten by nearly all rats in the 1975 savannah sample, this plant occurred in no food quadrats, and I found only two small patches of it in the 5.1 ha grid. *Solanum nodiflorum* was uncommon in the montane forest and was absent from all food quadrats during both trapping periods; however, its berries had been eaten by 20 percent of the rats caught in 1976 and by 12 percent of those caught in 1974. In 1974 in the montane forest, *Zanthoxylum fagara* seeds were eaten by 33 percent of the rats trapped, but these seeds were rarely seen and occurred in none of the food quadrats. Furthermore, for no population

was there a significant correlation between the abundance of a food (frequency in quadrats) and its frequency of occurrence in rat stomachs (all foods in the diet for which I had an abundance value; Spearman's  $r_s = 0.13-0.27$ ,  $P > 0.05$  in all cases).

Two distinct patterns of selectivity are illustrated by the savannah data presented in table 1. First, as indicated above, fleshy fruits are highly preferred, even at low abundances. Second, *R. rattus* clearly discriminates among equivalent parts of different plants. While all rats in this sample had eaten *Mentzelia* seeds, only 9 percent had eaten *Blainvillea* seeds, which were at least as abundant. Such discrimination among seeds was also exhibited by the 1974 thorn scrub sample; none of the rats ( $N = 34$ ) had eaten *Ipomoea triloba* seeds (present in 11/50 quadrats), while over half had eaten the much less abundant seeds of *Bastardia viscosa* (present in 1/50 quadrats).

**DIET DIFFERENCES AMONG HABITATS.**—The usage of general categories of foods differed among habitats (figs. 2-4). Seeds, leaves, and flowers were eaten in considerable amounts only by the rats from the two

arid habitats (thorn scrub and savannah), and vertebrates were eaten only in these sites. Fungi were important only in the diet of the montane forest rats.

Some of these differences result from the occurrence of certain food types only in particular habitats. Fungi were abundant only in the montane forest. Similarly, intact seeds occurred infrequently in quadrats in the wet, montane habitats, while they were abundant in the dry sites (most seeds found in the moist litter of the wet sites were rotten). Rapid decomposition of carrion in the wet habitats may explain why vertebrate material occurred only in the diet of arid-site populations.

Leaves and flowers were present in all the habitats; thus simple availability cannot account for their being dietarily important only in the dry sites. A probable explanation is that such foods are eaten when nutritionally richer foods are scarce.

The responses to one food, *Ipomoea triloba* seeds, differed strikingly between rat populations of the two dry sites. These seeds were heavily used by the rats in the 1975 savannah sample (appendix 1). Although *I. triloba* seeds were equally abundant in the thorn scrub when black rats were sampled there in 1974 (frequency in quadrats = 22%, compared with 24% in the savannah), none of the rats ( $N = 34$ ) had eaten these seeds. The explanation for such a pronounced difference in feeding responses to these seeds seems unlikely to be differential availability of alternative foods. Possibly, either the *I. triloba* seeds of the thorn scrub (Pinzón I.) are considerably more toxic, or the *R. rattus* of the savannah (San Salvador I.) are more tolerant of *I. triloba* toxins.

**DIETARY SHIFTS WITHIN HABITATS.**—In each habitat the diet differed greatly between seasons (figs. 2-4; appendix 1). Many of these differences reflect the marked seasonality of particular foods, such as *Psy-*

TABLE 1. Preferential feeding by the 1974 savannah *R. rattus* population, as indicated by the lack of correspondence between the usage of certain foods and their abundance.

Food	Frequency of occurrence (%)	
	In quadrats (N = 50)	In rats (N = 11)
Seeds		
<i>Blainvillea dichotoma</i>	28	9
<i>Sida</i> spp.	36	55
<i>Bursera graveolens</i>	16	82
<i>Mentzelia aspera</i>	22	100
Fleshy fruits		
<i>Tournefortia psilostachya</i>	4	91
<i>Physalis</i> spp.	6	91

TABLE 2. Seasonal abundances and consumption patterns of selected foods of Galápagos black rats.

Food	Habitat	Date	Frequency of occurrence (%)	
			In quadrats (N)	In rats (N)
<i>Psychotria rufipes</i> (fruit)	Montane forest	Sept. 1974	44 (50)	100 (49)
		Apr. 1976	1 (100)	13 (30)
<i>Mentzelia aspera</i> (seed)	Savannah	May 1974	22 (50)	100 (11)
		Nov. 1975	2 (50)	13 (15)
		May 1974	36 (50)	55 (11)
<i>Sida</i> spp. (seed)	Savannah	Nov. 1975	8 (50)	0 (15)
		Sept. 1974	52 (100) <sup>a</sup>	0 (49)
		Apr. 1976	37 (100) <sup>a</sup>	63 (30)
<i>Commelina diffusa</i> (stem)	Montane forest	May 1974	6 (50)	100 (11)
		Nov. 1975	2 (50)	20 (15)

<sup>a</sup>Data from vegetation quadrats of D. B. Clark (pers. comm.).

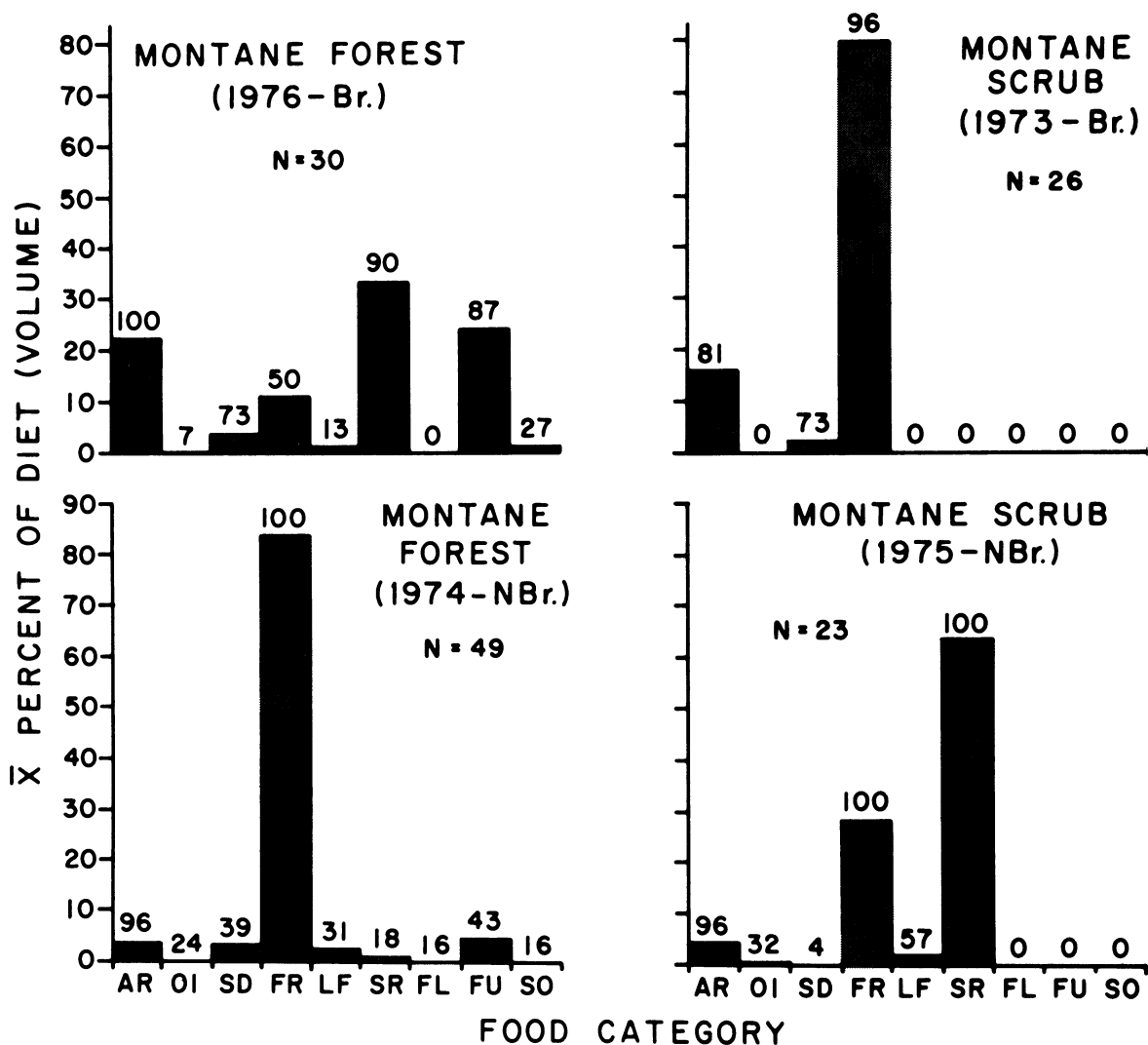


FIGURE 2. The composition of the diet of breeding (Br.) and non-breeding (NBr.) populations in the montane forest and montane scrub sites. For each food category the mean percent (by volume) of the diet is shown by the height of the bar; the frequency of occurrence (%) in individuals is indicated above each category. Food categories: arthropod (AR); other invertebrates (OI); seed (SD); fruit (FR); leaf (LF); stem, root, and rhizome (SR); flower (FL); fungus (FU); soil and litter (SO).

*chotria* fruits and *Mentzelia* and *Sida* seeds (table 2). In some cases, however (e.g., *Commelina* stem and *Physalis* fruit; table 2), there was no relationship between the abundance of the food and its consumption during the two seasons. These seasonal differences in feeding response could be due to chemical changes in the food, the availability of alternate foods, or changes in feeding preferences related to reproduction or water availability.

The two samples from the 1975 breeding season in the thorn scrub (fig. 4, appendix 1) illustrate the rats' capability for rapid diet shift. These two

groups were trapped three weeks apart, during a period of dramatic vegetation change due to heavy rains. While fruits and leaves were negligible in the diet of the first sample, the diet of the rats trapped three weeks later contained considerable amounts of fruits and leaves and included eight new species of plants. There were also significant differences between groups in the amount of arthropods eaten and of *Croton scouleri* seeds (Mann-Whitney  $U = 0$  and 3;  $P = 0.004$  and 0.03, respectively).

**SEED PREDATION.**—I identified fruits or seeds of 51 species of plants in the stomachs of Galápagos



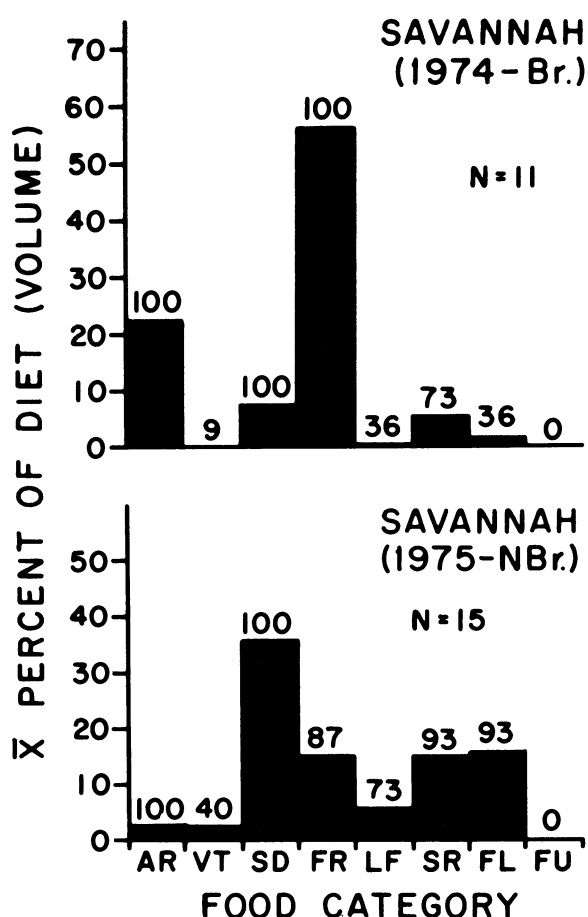


FIGURE 3. The composition of the diet of breeding (Br.) and non-breeding (NBr.) populations in the savannah site. For each food category the mean percent (by volume) of the diet is shown by the height of the bar; the frequency of occurrence (%) in individuals is indicated above each category. Food categories: arthropod (AR); vertebrate (VT); seed (SD); fruit (FR); leaf (LF); stem, root, and rhizome (SR); flower (FL); fungus (FU).

black rats (appendix 1). For 39 species, the rats are clearly seed predators; all or nearly all the seeds had been chewed and crushed. In a few cases, however, most seeds are left intact. The rats discard the seeds when they eat the fleshy fruits of *Psychotria rufipes* and *Castela galapageia*. The seeds are ingested in large numbers but few or none are chewed, when the fleshy fruits of *Passiflora foetida*, *Solanum nodiflorum*, and *Miconia robinsoniana* are eaten (however, young black rats do crush *Miconia* seeds; see D. A. Clark 1980). In the case of berries of *Physalis pubescens* and *P. galapagoensis*, although many seeds are destroyed, many others pass through intact. A similar situation occurs with the small fruits of grasses

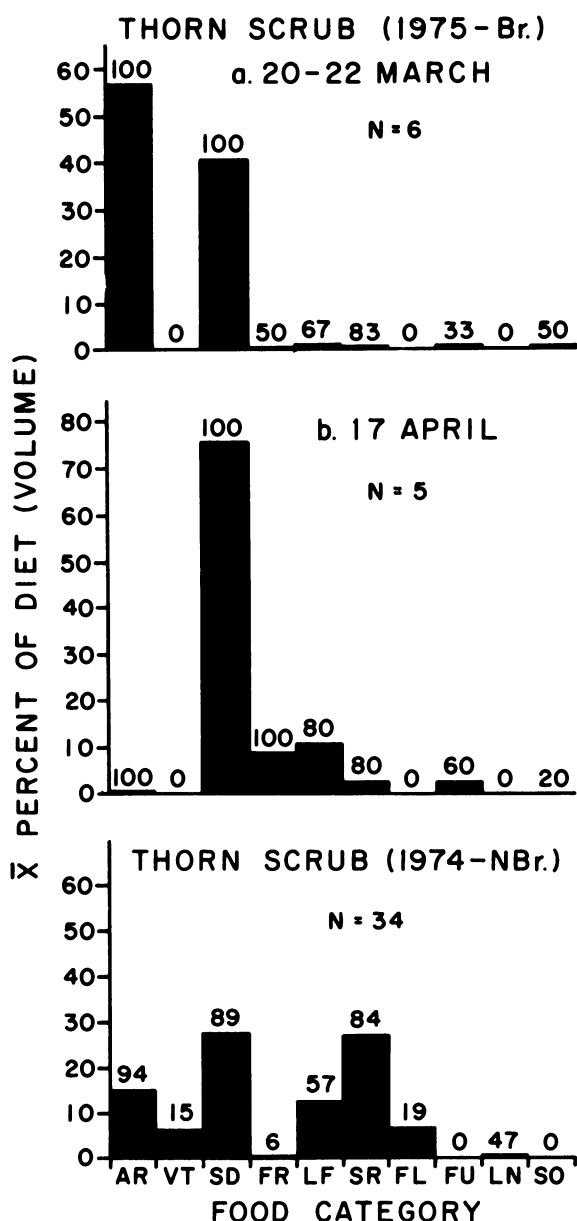


FIGURE 4. The composition of the diet of the two breeding samples (Br.) and the non-breeding population (NBr.) in the thorn scrub site. For each food category the mean percent (by volume) of the diet is shown by the height of the bar; the frequency of occurrence in individuals (%) is indicated above each category. Food categories: arthropod (AR); vertebrate (VT); seed (SD); fruit (FR); leaf (LF); stem, root, and rhizome (SR); flower (FL); fungus (FU); lichen (LN); soil and litter (SO).

(*Aristida* spp., *Ichnanthus nemorosus*, and *Panicum fasciculatum*), and of *Pilea bauri*. When the fruits of the orchid *Epidendrum spicatum* are eaten, the minute seeds reach the stomach intact. I have no data

on the germination potential of seeds that pass through the gut of black rats intact [whole seeds of *Lycopersicon cheesmanii* extracted from feces of Galápagos black rats did not germinate (Rick 1966)].

**ANIMAL FOODS IN THE DIET.**—The strong propensity of Galápagos *R. rattus* to eat animal foods is indicated by the very high frequency of occurrence of these foods in stomachs (figs. 2-4). All or nearly all stomachs contained some animal matter, even in populations where the average volume of animal food was very low (e.g., the 17 April 1975 thorn scrub sample; fig. 4); also, the volume of animal food will usually be underestimated, due to protein digestion in the stomach. A strong propensity to eat animal foods, even when their availability is low, would be highly adaptive for an omnivore. The protein provided by animal tissues is of higher quality (in terms of amino acid balance) than most plant proteins (Needham 1964).

The animal foods eaten varied among populations. Snails and earthworms were eaten only by rats sampled in the two humid-zone sites (montane scrub and montane forest). A green stinkbug (Pentatomidae) was preyed on in both montane sites; in August 1975 these insects were common in the montane scrub (2.04/m<sup>2</sup>), and 96 percent of the rats had eaten them (a minimum of 1.15/stomach, estimated from appendages). Lepidopteran larvae were commonly taken in all habitats. Ants were eaten by individuals in most samples, but they were often found mixed with bait, and may have been eaten only incidentally. Very small individuals of the Galápagos centipede, *Scolopendra galapagoensis*, were eaten by rats in the thorn scrub and in the montane scrub.

Vertebrate matter seldom occurred in stomachs (other than material from rats or mice eaten out of traps). None was found in the 250 montane-zone rats, and more than trace amounts were present in only eight of the 90 arid-zone rats analyzed. Goat or burro remains were identified in two 1975 savannah rats. The birds and small reptiles in the rat stomachs could have been either preyed upon by the rats or eaten as carrion. The only vertebrates definitely known to be killed by Galápagos black rats are hatchlings of the giant tortoise, *Geochelone elephantopus* (MacFarland *et al.* 1974; pers. obs.).

**REPRODUCTION AND ANIMAL FOOD IN THE DIET.**—In all Galápagos habitats where they have been studied, black rats are highly seasonal breeders; their reproductive activity is confined to the hot season and early garúa season (D. B. Clark 1980). Because I determined the diet of population samples from both the breeding and the non-breeding seasons

in each site, I can examine the relationship of diet to reproduction.

One nutritional demand for reproduction is a relatively high intake of balanced protein (Russell 1948, Hsueh *et al.* 1967). In three of the four habitats studied, the average percent animal food in the stomach (for adult-sized rats; see Methods) was much higher for breeding than for non-breeding samples (table 3). Among the montane forest, montane scrub, and savannah populations there was a striking similarity in the levels of animal food within each season. The non-breeding populations averaged only 17-35 percent as much animal food as the breeding populations. For these quite different habitats, then, the evidence is consistent with the hypothesis that black rat reproduction requires an elevated level of high-quality protein in the diet.

TABLE 3. Mean percent animal food (by volume) in the diet of breeding and non-breeding *R. rattus* populations in the four study sites. Sample size is given in parentheses.

Habitat	Season	
	Breeding	Non-breeding
Montane forest	22.15 (30)	3.84 (49)
Montane scrub	16.06 (26)	5.57 (23)
Savannah	22.40 (11)	5.50 (15)
Thorn scrub	56.37 (6) <sup>a</sup> 0.60 (5) <sup>b</sup>	21.23 (34)

<sup>a</sup>20-22 March 1975.

<sup>b</sup>17 April 1975.

In the thorn scrub the level of animal food in the diet was as high during the non-breeding season as it was in the breeding period in the other habitats. Evidently, high animal food intake is not sufficient for black rat reproduction, at least in the thorn scrub. Water may be a limiting factor; in the cool season, succulent fruits are absent from this habitat.

The thorn scrub rats also differed in their breeding-season diet (in spite of small sample size, the extreme similarity in diet among individuals in each sample allows meaningful comparisons). The stomachs of all individuals in the first breeding-season sample contained at least 40 percent arthropods (primarily lepidopteran larvae); however, in the second sample, trapped 21 days later, no rats had more than 1 percent animal food in the stomach (the presence of a pregnant female demonstrated continuing reproduction). Although this sample seems to negate the necessity of high dietary protein for breeding, such a conclusion may be unwarranted. *Croton scouleri* seeds comprised 40-96 percent of the stomach contents of these rats, and the endosperm of these seeds



(with the seed coat removed) is high in crude protein (33% of dry matter). If the amino acid complement is well-balanced, these seeds could be replacing arthropods as a source of high-quality protein in the rats' diet.

Taken together, the data from these four habitats show that breeding occurred only during periods of (relatively) high protein intake. Lacking information on the quantity of high-protein food available, I cannot establish if breeding is restricted to periods of availability of high-protein food, or if breeding is seasonal because of some other factor(s), and the difference in levels of high-protein food intake is due to a shift in foraging behavior rather than to changing food availability.

If protein is one limiting factor for breeding, the thorn scrub non-breeding population indicates there is at least one other factor, such as water availability. There are no obvious relationships between any other classes of food and occurrence of breeding for these rat populations (figs. 2-4). It has been suggested that green vegetation in the diet is important for reproduction of desert heteromyids (Beatley 1969, Bradley and Mauer 1971, Reichman and Van de Graff 1975). My data show no evidence of such a relationship for Galápagos *R. rattus*.

## DISCUSSION

A fundamental aspect of Galápagos black rat feeding behavior is their ability to use a very broad range of foods, both within and among different habitats. Such dietary versatility has also been documented for *R. rattus* populations in other parts of the world, including Hawaii (Kami 1966), New Zealand (Best 1969, Daniel 1973), Australia (Watts and Braithwaite 1978), the Philippines (Tigner 1972), and Eniwetok Atoll (Fall *et al.* 1971).

Although the foods eaten are extremely diverse, the important items in the diet of Galápagos black rats tend to be nutritionally superior. Predominant plant foods are fruits and starch-filled rhizomes, which are high in digestible carbohydrates, and seeds, which are often high in fats and protein. The animal foods in the diet are sources of balanced protein. Leaves and fibrous stems, less nutritious potential foods, are not heavily used by these rats. This pattern of preferential feeding on high-quality foods has also been borne out by the previous studies of black rat feeding (references given above).

The similarity between the foods eaten in the Galápagos and those consumed in other parts of the world is striking. Plants eaten both in the Galápagos and in the Philippines (Tigner 1972) include *Com-*

*melina diffusa* and species of *Physalis*, *Ipomoea*, *Paspalum*, *Alternanthera*, and *Sida*. *Solanum* sp. berries were also consumed by black rats in Hawaii (Kami 1966) and New Zealand (Daniel 1973). *Tournefortia* sp. fruits and an *Ipomoea* species were also eaten by *R. rattus* on Eniwetok Atoll (Fall *et al.* 1971). Fungi, an important food of the Galápagos montane forest populations, are also commonly eaten by black rats in Tasmania (Norman 1970), mainland Australia (Watts and Braithwaite 1978), and New Zealand (Daniel 1973).

One apparently distinctive feeding pattern of *Rattus* in Galápagos is the extremely high frequency of occurrence of animal food in stomachs (mean = 96%; range = 81-100%). In most other studies of this species, a much lower proportion of individuals analyzed were found to have animal foods in their stomach (28%, Strecker and Jackson 1962; 12-18%, Kami 1966; 38%, Fall *et al.* 1971; 68%, Tigner 1972; 23-79%, Daniel 1973). It is not clear whether the Galápagos rats actually differ from others in their feeding behavior or whether the inconsistency results from differences in stomach contents analysis.

## IMPACT OF BLACK RATS ON GALÁPAGOS ECOSYSTEMS

**IMPACT ON THE FLORA.**—A combination of factors increases the probability of significant impacts on Galápagos plant communities by these introduced omnivores: (1) in Galápagos, black rats are primarily herbivorous; (2) they prefer the reproductive structures of plants; (3) they destroy nearly all seeds ingested; and (4) they often concentrate on relatively uncommon species. The black rats' selectivity in feeding may also considerably affect plant species composition. Although there is general recognition of the severe effects on the Galápagos flora caused by large introduced herbivores, such as goats (Hamann 1975, deVries and Calvopiña (1977)), the potential impacts of black rats also warrant investigation.

**IMPACT ON GALÁPAGOS ANIMALS.**—Even though animal foods comprise a low proportion of their diet, black rats have severe effects on Galápagos vertebrates. They have apparently caused the extinction of several native rat species (Brosset 1963), perhaps by introducing new parasites or disease. Their predation on Pinzón hatchling tortoises prevents any natural recruitment in that tortoise population (MacFarland *et al.* 1974). In addition, the continued reproductive failure of endangered dark-rumped Petrels (*Pterodroma phaeopygia*) on Santa Cruz Island is thought to be due to destruction of eggs and chicks by *R. rattus* (Harris 1970).

In this study, few of the rats analyzed had eaten

vertebrates. Remains of several endemic Galápagos reptiles (gecko, *Phyllodactylus galapagensis*; lava lizards, *Tropidurus* spp.; and snakes, *Dromicus* sp.) were identified in black rat stomachs; however, in most cases, this material occurred in only trace amounts. These occurrences may represent feeding on carrion rather than predation. The few instances of bird remains (largely feathers) in stomachs may also have resulted from scavenging. It is nevertheless important to recognize that even infrequent predation on vertebrates by black rats could have a significant impact. For example, in the 1974 thorn scrub sample, 6% of the rats had eaten birds; at the highest density of rats recorded in this habitat (19/ha in November 1975; D. B. Clark 1980), predation at this rate could account for 34 birds/ha/month. Unfortunately, the extent to which *R. rattus* does, in fact, actively prey on Galápagos vertebrates (other than hatchling tortoises) remains unknown.

Predation on invertebrates is an important facet of the foraging of Galápagos black rats, with a wide variety of invertebrates taken in all habitats. This predation may be significantly affecting some of the prey. Extrapolation from minimum feeding rates on a distinctive pentatomid bug by the 1975 montane scrub rats (1.15 bugs/rat) and the density of rats (15.4/ha; D. B. Clark 1980) and prey (20,400/ha) indicates the rats could be eating at least 3 percent of the standing crop in a month. Tjitte deVries (pers. comm.) once watched a black rat catch and eat 127 moths in an hour, at a window at the Darwin Station. Several of my study populations preyed heavily on lepidopteran larvae. The quantitative effect of *R. rattus* predation on invertebrates, particularly on the endemic forms, should be studied.

In addition to direct impacts on the Galápagos fauna, black rats may be having important indirect effects on native animals whose foods they eat. On Pinzón Island, for example, the rats may be competing with the granivorous doves and finches for the very rich *Croton* seeds. In the *Scalesia* forest, the rats may be reducing the biomass and diversity of fruits available to the vegetarian tree finch (*Platyspiza crassirostris*).

**RELATIVE VULNERABILITY OF GALÁPAGOS HABITATS.**—The effect of introduced black rats, once they are established, is likely to be much more important in those Galápagos ecosystems which never supported

a native rice rat (*Oryzomys* or *Nesoryzomys* spp.). The extinct native rats were probably quite similar to black rats in their ecological role. Where they have been studied elsewhere, *Oryzomys* spp. were shown to feed on a wide range of plants and animals (Hamilton 1946, Negus *et al.* 1961, Sharp 1967), and *O. palustris* was even found to prey heavily on hatchlings of several species of turtles (Goodpaster and Hoffmeister 1952). To the extent that the diet of the native rats paralleled that of *R. rattus*, the impact of black rats should be most severe where native rats never occurred (e.g., Pinzón Island); in fact, Pinzón is the only site where black rats are known to prevent tortoise recruitment by their predation on hatchlings (MacFarland *et al.* 1974).

## CONCLUSIONS

Several aspects of black rat feeding ecology in Galápagos serve as a partial explanation for this species' success in such a broad range of environments. Probably the most important factor is the flexibility and breadth of diet displayed by these animals. Galápagos *R. rattus* are able to obtain adequate diets in a range of habitats with extremely different spectra of available foods. Their preferential feeding on energy- and nutrient-rich foods must also contribute to their success in achieving adequate nutrition in these environments. Finally, their apparent predisposition to eat animal matter would promote intake of balanced protein, a probable limiting factor for reproduction. With their great diet breadth and their highly preferential feeding behavior, black rats may be causing many severe impacts on the flora and fauna of the Galápagos Islands.

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APPENDIX 1. Composition of the diet of Galápagos black rat populations. Frequency of occurrence = percent of stomachs in which the food occurs. Foods found only in stomachs that were excluded from the analysis (see Methods) are indicated with an asterisk.

Food type		Frequency of occurrence	Mean % volume
Montane forest, April 1976 (N = 30)			
<i>Blechnum occidentale</i>	rhizome	20.0	8.55
<i>Canna lambertii</i>	seed	23.3	1.52
<i>Commelina diffusa</i>	stem	63.3	15.40
	leaf	6.7	0.98
<i>Elaterium carthagenense</i>	leaf	3.3	0.02
<i>Epidendrum spicatum</i>	fruit, seed	30.0	7.05
<i>Ichnanthus nemorosus</i>	seed	6.7	0.03
	leaf	3.3	0.13
<i>Musa x paradisiaca</i>	fruit	3.3	2.32
<i>Psychotria rufipes</i>	fruit	13.3	0.17
	seed	16.7	0.08
<i>Scaevola pedunculata</i>	seed	53.3	1.74
<i>Sida</i> sp.	seed	3.3	0.02
<i>Solanum nodiflorum</i>	fruit, seed	20.0	1.60
<i>Tournefortia</i> sp.	seed	3.3	0.03
Unidentified	seed	16.7	0.23
	stem	23.3	4.72
	root/rhizome	13.3	4.67
	leaf	3.3	0.03
Fungi (many types, unidentified)		86.7	24.11
Arthropod		100.0	22.10
Earthworm		3.3	0.02
Snail		6.7	0.03
Soil/litter		26.7	1.44
Liverwort (unidentified)		53.3	0.51
Additional, unidentified material		60.0	2.52

Montane forest, September 1974 (N = 49)

<i>Acnistus ellipticus</i>	seed	4.1	0.02
<i>Blechnum occidentale</i>	rhizome	2.0	0.73
<i>Canna lambertii</i>	seed	2.0	0.06
<i>Elaterium carthagenense</i>	leaf	26.5	2.52
<i>Ichnanthus nemorosus</i>	seed	2.0	0.01
<i>Pilea baurii</i>	fruit	4.1	0.02
<i>Psychotria rufipes</i>	fruit, seed	100.0	82.61
	leaf	2.0	0.01
	flower	4.1	0.02
<i>Solanum nodiflorum</i>	fruit, seed	12.2	0.38
<i>Tournefortia</i> sp.	fruit, seed	6.1	0.04
<i>Zanthoxylum fagara</i>	seed	32.7	3.50
Unidentified	stem	16.3	0.40
	flower	10.2	0.12
	fruit	10.2	0.89

fern frond	2.0	0.10
seed	28.6	0.15
Fungi (many types, unidentified)	42.9	4.84
Arthropod	95.9	3.62
Earthworm	8.2	0.11
Snail	18.4	0.11
Litter	16.3	0.33
Additional, unidentified material	24.5	0.49

Montane scrub, April 1973 (N = 26)<sup>a</sup>

<i>Hibiscus diversifolius</i>	seed	3.8	0.04
<i>Miconia robinsoniana</i>	fruit, seed	96.2	79.92
<i>Paspalum conjugatum</i>	seed	69.2	2.17
Arthropod		80.8	16.06
Unidentified material		23.1	2.19

Montane scrub, August 1975 (N = 23)

<i>Blechnum polypodioides</i>	rhizome	100.0	57.35
<i>Commelina diffusa</i>	stem	21.7	2.57
	leaf	4.3	0.02
<i>Cyperus</i> sp.	leaf	4.3	0.04
<i>Jaegeria gracilis</i>	leaf	30.4	1.87
	stem	8.7	3.30
	flowers	*	*
<i>Lobelia xalapensis</i>	leaf	4.3	0.02
<i>Lycopodium</i> sp.	leaf	8.7	0.04
	stem	*	*
<i>Mecardonia dianthera</i>	leaf	13.0	0.33
<i>Miconia robinsoniana</i>	fruit, seed	100.0	28.17
<i>Paspalum conjugatum</i>	seed	8.7	0.04
<i>Solanum nodiflorum</i>	fruit, seed	13.0	0.09
Unidentified	leaf	4.3	0.02
	stem	8.7	0.39
Arthropod		95.7	4.63
Snail (and egg masses)		17.4	0.20
Earthworm		30.4	0.74
Additional, unidentified material		30.4	0.50

Savannah, May 1974 (N = 11)

<i>Abutilon depauperatum</i>	seed	*	*
<i>Amaranthus</i> sp.	seed	9.1	0.05
	leaf	9.1	0.44
<i>Anthephora hermaphrodita</i>	seed	9.1	0.09
<i>Blainvillea dichotoma</i>	seed	9.1	0.05
<i>Blechnum brownei</i>	fruit, seed	45.5	9.78
<i>Boerhaavia caribaea</i>	leaf	9.1	0.05
<i>Bouteloua disticha</i>	leaf	9.1	0.05
	seed	*	*
<i>Bursera graveolens</i>	seed and aril	81.8	9.61
<i>Castela galapageia</i>	seed	*	*
<i>Chamaesyce</i> sp.	seed	*	*
<i>Cordia lutea</i>	seed	27.3	0.14
<i>Heliotropium angiospermum</i>	fruit	9.1	0.05
<i>Ipomoea triloba</i>	seed	45.5	0.31

## APPENDIX 1. (Continued)

<i>Lantana peduncularis</i>	fruit, seed	*	*
<i>Mentzelia aspera</i>	seed	100.0	1.79
<i>Passiflora suberosa</i>	flower	27.3	1.74
	fruit, seed	*	*
<i>Physalis galapagoensis</i> and <i>P. pubescens</i>	fruit, seed	100.0	17.31
	leaf	*	*
<i>Portulaca oleracea</i>	seed	*	*
<i>Sida</i> sp.	seed	54.5	0.27
<i>Tetramerium nervosum</i>	seed	9.1	0.05
<i>Tournefortia psilostachya</i>	fruit, seed	90.9	19.13
Unidentified	seed	90.9	4.65
	leaf	9.1	0.09
	flower	9.1	0.09
	stem	72.7	5.18
Fungus		9.1	0.05
Arthropod		100.0	22.35
Lizard ( <i>Tropidurus albemarlensis</i> )		9.1	0.05
Additional, unidentified material		45.5	6.62
Savannah, November 1975 (N = 15)			
<i>Acacia macracantha</i>	leaf	46.7	4.00
	flower	6.7	0.03
<i>Aristida</i> sp.	seed	6.7	0.03
<i>Blechnum brownei</i>	fruit, seed	13.3	0.27
	flower	6.7	0.03
<i>Castela galapageia</i>	fruit	6.7	0.03
<i>Chamaesyce</i> sp.	seed	6.7	0.03
	leaf	13.3	0.98
<i>Commicarpus tuberosus</i>	leaf	6.7	0.03
<i>Cordia lutea</i>	fruit, seed	60.0	8.03
<i>Crotalaria pumila</i>	seed	13.3	0.10
<i>Heliotropium angiospermum</i>	leaf	6.7	0.20
<i>Ipomoea triloba</i>	seed	86.7	34.90
<i>Mentzelia aspera</i>	seed	13.3	0.07
<i>Passiflora suberosa</i>	fruit, seed	73.3	2.98
	flower	80.0	14.81
<i>Physalis galapagoensis</i> and <i>P. pubescens</i>	fruit	20.0	3.61
	seed	60.0	0.30
<i>Porophyllum ruderale</i>	seed	6.7	0.03
<i>Sida</i> sp.	seed	*	*
<i>Tetramerium nervosum</i>	leaf	13.3	0.07
Unidentified	seed	20.0	0.10
	fruit	13.3	0.07
	leaf	46.7	0.27
	stem	93.3	14.84
	flower	46.7	0.23
Arthropod		100.0	2.85
Lizard ( <i>Tropidurus albemarlensis</i> )		13.3	0.07
Reptile (unidentified)		6.7	0.03
Bird (unidentified)		6.7	0.32
Carrion of goat or burro		13.3	2.23
Additional, unidentified material		66.7	8.48

## Thorn scrub, 20-22 March 1975 (N = 6)

<i>Alternanthera echinocephala</i>	leaf	16.7	0.08
<i>Croton scouleri</i>	seed	100.0	40.50
<i>Grabowskia boerhaaviaefolia</i>	leaf	16.7	0.33
<i>Heliotropium angiospermum</i>	leaf	33.3	0.25
<i>Merremia aegyptica</i>	seed	16.7	0.08
<i>Panicum fasciculatum</i>	seed	*	*
<i>Portulaca umbraticola</i>	leaf	16.7	0.17
Unidentified	fruit	50.0	0.33
	stem	83.3	0.57
	leaf	33.3	0.17
Fungus		33.3	0.91
Arthropod (primarily lepidopteran larvae)		100.0	56.37
Soil		50.0	0.25

## Thorn scrub, 17 April 1975 (N = 5)

<i>Alternanthera echinocephala</i>	leaf	20.0	4.20
<i>Alternanthera</i> sp.	stem	20.0	0.20
<i>Chamaesyce</i> sp.	leaf	40.0	2.30
<i>Croton scouleri</i>	seed	100.0	74.60
<i>Grabowskia boerhaaviaefolia</i>	leaf	60.0	3.20
<i>Lantana peduncularis</i>	fruit, seed	100.0	6.60
<i>Oxalis cornellii</i>	seed	20.0	0.10
<i>Panicum fasciculatum</i>	seed	20.0	0.10
<i>Panicum hirticaule</i>	seed	20.0	0.10
<i>Physalis galapagoensis</i>	seed	80.0	0.50
<i>Portulaca umbraticola</i>	seed	40.0	0.20
	leaf	20.0	0.10
<i>Tournefortia psilostachya</i>	fruit, seed	20.0	2.00
<i>Trianthema portulacastrum</i>	leaf	20.0	0.80
	seed	40.0	0.20
Unidentified	stem	60.0	2.00
	leaf	20.0	0.10
Fungus		60.0	2.20
Soil/pebbles		20.0	0.10
Arthropod		100.0	0.60
Additional, unidentified material		80.0	0.70

## Thorn scrub, January 1974 (N = 34)

<i>Acacia macracantha</i>	leaf	*	*
	flower	*	*
<i>Alternanthera echinocephala</i>	leaf	11.8	2.61
	flower	2.9	0.12
	stem	2.9	0.06
<i>Alternanthera filifolia</i>	leaf	29.4	4.49
	stem	35.3	7.89
<i>Alternanthera</i> sp.	stem	2.9	0.03
<i>Bastardia viscosa</i>	seed	52.9	0.39
<i>Croton scouleri</i>	seed	2.9	0.01
	male flower	17.6	6.35
	leaf	2.9	0.01



APPENDIX 1. (Continued)				Unidentified	stem	76.5	14.47
<i>Desmanthus virgatus</i>	seed	2.9	0.01		seed	8.8	0.04
<i>Evolvulus glaber</i>	seed	41.2	1.29		leaf	8.8	0.34
	leaf	8.8	0.06		fruit	2.9	0.03
<i>Grabowskia</i>	leaf	14.7	3.31	Lichen		47.1	0.45
<i>boerhaaviaefolia</i>				Arthropod		94.1	15.13
	fruit	2.9	0.03	Lizard ( <i>Tropidurus duncanensis</i> )		5.9	2.59
<i>Merremia aegyptica</i>	seed	5.9	0.03	Gecko ( <i>Phyllodactylus galapagensis</i> )		2.9	0.26
<i>Parkinsonia aculeata</i>	seed	14.7	8.17	Bird		5.9	3.25
<i>Prosopis juliflora</i>	seed	47.1	17.70	Additional, unidentified material		55.9	4.43
	buds	17.6	2.23				
	leaf	*	*				
<i>Setaria geniculata</i>	stem	5.9	2.31				
<i>Tournefortia psilostachya</i>	leaf	2.9	0.01				
<i>Zanthoxylum fagara</i>	leaf	2.9	1.90				

\*Diet diversity in this population (1973 montane scrub) may be underestimated, due to the technique of stomach analysis used for this sample (see Methods).

## Announcement: XVth Pacific Science Congress, 1983

The XVth Pacific Science Congress will be held in Dunedin, New Zealand, 1-11 February 1983. The theme is to be "Conservation, Development, and Utilization of the Resources of the Pacific."

A session is planned on the diversity, distribution, abundance, and management of vertebrate populations in the Pacific region. Joint sessions will be arranged with related disciplines. Speakers are now invited to offer papers (with title and short summary) on such topics as: Biogeography, Species diversity, Habitat requirements, Migration and movements, Population ecology, Ecosystem studies, Man-induced changes, Endangered species, and Conservation and management.

For further information, please write to Dr. C. W. Burns, Section Convener (Ecology and Environmental Protection), c/o Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand.