

## Food Habits of Introduced Rodents in High-Elevation Shrubland of Haleakalā National Park, Maui, Hawai'i<sup>1</sup>

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**ABSTRACT:** *Mus musculus* and *Rattus rattus* are ubiquitous consumers in the high-elevation shrubland of Haleakalā National Park. Food habits of these two rodent species were determined from stomach samples obtained by snap-trapping along transects located at four different elevations during November 1984 and February, May, and August 1985. *Mus musculus* fed primarily on fruits, grass seeds, and arthropods. *Rattus rattus* ate various fruits, dicot leaves, and arthropods. Arthropods, many of which are endemic, were taken frequently by *Mus musculus* throughout the year at the highest elevation where plant food resources were scarce. Araneida, Lepidoptera (primarily larvae), Coleoptera, and Homoptera were the main arthropod taxa taken. These rodents, particularly *Mus musculus*, exert strong predation pressure on populations of arthropod species, including locally endemic species on upper Haleakalā Volcano.

DISPERSED BY HUMAN commerce, the omnivorous rodents *Rattus* spp. and *Mus musculus* have become widely established on islands of the world, where they contribute substantially to the impoverishment of native island biota (Best 1969, Clark 1981, Atkinson 1985, 1989, Rowe-Rowe et al. 1989, Smith and Steenkamp 1990, Amarasekare 1993). As in other isolated oceanic archipelagoes, the fauna and flora of the Hawaiian Islands are highly vulnerable to human-facilitated invasions as a result of long evolution in isolation (Howarth 1985, Loope and Mueller-Dombois 1989, Cuddihy and Stone 1990). Hawai'i's endemic biota has been largely

eliminated in the lowlands, but survives in a relatively undisturbed state in certain middle- and high-elevation areas (Scott et al. 1986). One such area is the high-elevation shrubland of Haleakalā National Park on the island of Maui. As a result of intensive management efforts for conservation of native biota, some of the major impacts of introduced mammals (e.g., cattle, goats, pigs) have been removed from this ecosystem (Stone and Loope 1987).

Three species of rats (*Rattus rattus*, *R. exulans*, and *R. norvegicus*) and one species of mouse (*Mus musculus*) inhabit Hawaiian ecosystems (Tomich 1986). The rat species have been implicated in the decline of native Hawaiian flora and fauna (plants: Stone [1985]; snails: Hadfield et al. [1993]; birds: Atkinson [1985], Simons [1985], Amarasekare [1993]) and are likely influential in the decline of native invertebrate populations (Gagné and Christensen 1985). The impacts of *Mus musculus* populations on the native biota have not been well documented, although their effects on native biota may be more important than that of *Rattus rattus*, especially during population irruptions (Sugihara 1997).

Only *Mus musculus* and *Rattus rattus* are

<sup>1</sup>This study was funded by the Western Region of the National Park Service and by grants from the Division of Natural Sciences and College Research Fund, Colby College. The Cooperative National Park Resources Studies Unit of the University of Hawai'i provided logistical support. Manuscript accepted 12 December 1999.

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common in the high-elevation shrubland (above 2000 m) of Haleakalā National Park (F.R.C., L.L.L., A.C.M., unpubl. data). These rodents reached the Hawaiian Islands in the early and late 1800s, respectively, probably as a result of commercial activity (Tomich 1986). The population dynamics of *Rattus rattus* and *Mus musculus* have been investigated in selected Hawaiian habitats (e.g., sugarcane fields [Tobin and Sugihara 1992], low- and mid-elevation forests on O'ahu and Hawai'i [Tamarin and Malecha 1971, 1972, Tomich 1986], montane rain forests [1600–2000 m (Sugihara 1997)], and high-elevation [ $>2000$  m] shrubland on Maui [F.R.C., L.L.L., A.C.M., unpubl. data]). The food habits of these species have been studied at lower elevations (Kami 1966, Fellows and Sugihara 1977, Russell 1980, Sugihara 1997), but not in the high-elevation shrubland.

The objectives of this study were to investigate the food habits of *Mus musculus* and *Rattus rattus* populations and to evaluate the potential effects of these introduced rodent species on the native biota of Haleakalā's high-elevation shrubland. The investigation reported here is part of a continuing program to understand the biology and ecological roles of alien species in Haleakalā National Park.

### Study Area

Haleakalā National Park is one of the most important sites in the Hawaiian Islands for preservation of endemic biota. It extends from sea level to 3056 m and protects rain forest, montane bogs, dryland forest, high-elevation grassland, and high-elevation shrubland. Feral pigs and goats affected the study area for many years but have been eliminated and kept out with the aid of fencing since the early 1980s. Our study was conducted in high-elevation shrubland at 2100–3000 m elevation on the western and northwestern slopes of Haleakalā Volcano within Haleakalā National Park (Figure 1). The high-elevation shrubland areas sampled are considered representative of an area of over 2000 ha within the park.

Mean annual rainfall on the western slope

of Haleakalā Volcano ranges from ca. 1000 to 2000 mm, decreasing with increasing elevation and lessening exposure to north-east trade winds (Giambelluca et al. 1986). Most precipitation falls during November–April; individual storms commonly drop over 200 mm within a 24-hr period. Mean monthly temperatures at Park Headquarters (2140 m elevation) range from 9.8°C in February to 13.5°C in July (U.S. Department of Commerce 1983–1988); mean monthly temperature at the mountain's summit (3056 m) is about 3–4°C lower. Freezing soil temperatures occur frequently and snow falls rarely at higher elevations (Noguchi et al. 1987).

Whiteaker (1983) subdivided the vegetation of upper Haleakalā into structural-floristic communities and described species composition at representative sites. Shrubs and grasses dominate the vegetation of upper Haleakalā Volcano (above 1950 m) on the northern and western flanks and extend to lower elevations (1200 m) on drier, leeward slopes. Native shrubs are common below 2500 m and become mixed with open grasslands at 2500–2700 m. Vegetation is sparse above 2700 m elevation. Soil is generally poorly developed, particularly at high elevation, on a substrate of cinder or volcanic rock.

Beardsley (1980) and Medeiros and Loope (1994) reported that the arthropod fauna in the study area contains a high number of very localized endemics, many living within the summit area of Haleakalā Volcano, including various species of flightless carabid beetles, lacewings, moths, and flies. These arthropod species are known to be threatened by alien social insect species (e.g., yellow-jacket [Gambino et al. 1987, 1990]; Argentine ant [Cole et al. 1992]). Invertebrates living in the study area are most conspicuous during April–June and least active during December–February (F.R.C., unpubl. data).

Birds are sparse in the high-elevation shrubland of Haleakalā Volcano. Two alien game bird species, the Ring-necked Pheasant (*Phasianus colchicus*) and the Chukar (*Alectoris chukar*), are the dominant avifauna in this ecosystem. Although these game birds overlap in distribution, habitat, and diet with

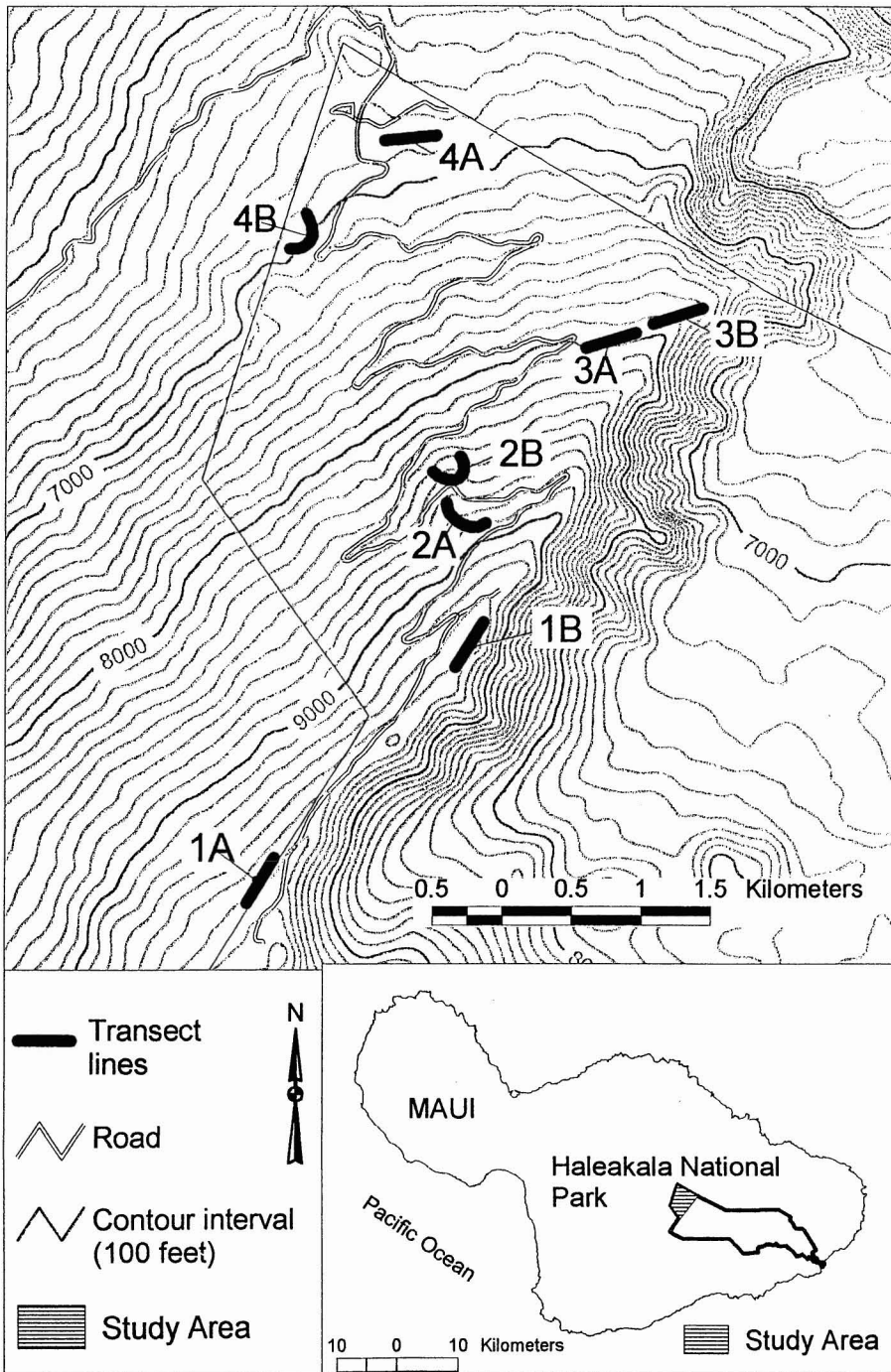


FIGURE 1. The western and northwestern slopes of Haleakalā Volcano showing the Haleakalā National Park boundary and study area. The location of each of the four study transects within the high-elevation shrubland is indicated.

*Mus musculus* and *R. rattus* (Cole et al. 1995), competition between rodents and game birds is probably low because of the general high abundance (and lack of obvious depletion) of major food items common to both groups (grass seeds, dicot fruits, and herbaceous vegetation). However, competition may be a factor in times of stress due to climate factors or population explosions. In addition to game birds, several passerine species are regularly seen in the study area, including Hawaiian endemic species, 'Amakihi (*Hemignathus virens*) and 'Apapane (*Himatione sanguinea*), and alien species, House Finch (*Carpodacus mexicanus*) and Japanese White-eye (*Zosterops japonicus*).

Predators of rodents are infrequently seen within the study area and include the introduced Indian Mongoose (*Herpestes auro-punctatus*), the feral cat (*Felis catus*), and the native Hawaiian Short-eared Owl (*Asio flammeus sandwichensis*). An extensive network of carnivore traps established as part of a program to protect the endangered Nēnē or Hawaiian Goose (*Nesochen sandvicensis*) and the Dark-rumped Petrel (*Pterodroma phaeopygia sandwichensis*) keeps the abundance of mongooses and feral cats low (Cathleen Hodges, Haleakalā National Park, pers. comm.).

#### MATERIALS AND METHODS

Linear transects totaling 750 m in length were established at each of four elevations at easily accessible sites along the main road to the summit of Haleakalā Volcano, on the mountain's northwestern slope in Haleakalā National Park. In choosing transect locations, an attempt was made to pass through vegetation representative of a given elevation. Transects were located at the following elevations: 1, 2860–2900 m; 2, 2640–2660 m; 3, 2430–2450 m; and 4, 2070–2130 m.

#### Vegetation

**SPECIES COMPOSITION.** A modified Braun-Blanquet relevé method (Mueller-Dombois and Ellenberg 1974) was used to characterize

the vegetation along the transects. Four quadrats, each 10 by 10 m in size, were established at approximately 120 m, 240 m, 500 m, and 620 m along the 750-m transects. A list of vascular plant species was compiled for each quadrat; nomenclature for vascular plant species follows Wagner et al. (1990). Cover of individual species was used as a measure of abundance and was estimated to the nearest 5% for visual comparison with a square frame representing 1 m<sup>2</sup> or 1% cover. Species occurring at less than 2.5% cover were assigned a cover value of 1%. Mean cover values were calculated using data from the four quadrats located along a transect and represent composite cover estimates as a measure of abundance of each plant species for that transect.

**PHENOLOGY.** Notes on occurrence (presence versus absence) and abundance (few versus many) of flowers, fruits, seeds, and succulent vegetation for plant species on each transect were made intensively at 3-month intervals (February, May, August, and November), with opportunistic observations at more frequent intervals throughout 1985. Specimens of leaf, seed, and fruit material were collected from the sites, identified, and stored as references for rodent food habits determinations.

#### Rodent Populations

**FIELD SAMPLING.** Fifty trapping stations, each consisting of two mouse traps (Victor) and one rat trap (Victor) and marked with flagging tape, were located at 15-m intervals along each transect. Traps were baited with small squares of fresh coconut, placed within 2 m of the station marker, and tended for 4–5 nights. Trapping was carried out along each transect on the following dates: 12–16 November 1984 and 11–14 February, 20–23 May, and 12–15 August 1985. Only *Mus musculus* and *Rattus rattus* were captured. Animals of representative age and sex classes were selected randomly from all captures at each transect for diet analysis.

**ANALYSIS OF STOMACH CONTENTS.** Food items were identified by comparing micro-

scopic examination of their cell structure with known reference samples. The contents of each stomach (only stomachs more than three-fourths full or stomachs containing less than 50% by volume of coconut were analyzed) were mixed and washed over a fine, bolting-silk screen to eliminate small, unidentifiable fragments. Wet-mount slides were prepared for diet analysis from randomly selected subsamples of the remaining contents. Percentage composition in the diet was estimated using a point sampling technique in which two slides (25 randomly selected points per slide) were examined for each stomach (Batzli and Pitelka 1971). The fragment closest to the center of the microscope field of view for each point was identified. In addition, the size of each fragment was estimated using an optical micrometer. Food habits were determined in two ways: percentage composition of the total sample points and relative abundance based on the size of each fragment sampled. Because both methods produced similar results, food habits are presented on a percentage composition basis. Statistical analyses of seasonal and elevational dietary patterns were conducted using *t*-tests. Data were transformed before analysis using an arcsine transformation (Zar 1984).

Many plant fragments were determined to species. Arthropod parts found in the stomach contents were identified by comparison with species known to occur in the study area based on extensive pitfall sampling conducted in the area. Identifications of arthropod reference species were made by entomologists at the Bishop Museum, Honolulu. Fragments were identified to the lowest taxon possible, in some cases to species but more commonly to family or order.

## RESULTS

### *Structure and Species Composition of Vegetation*

Relatively few native plant species occurred at the highest-elevation site (2860–2900 m; transect 1). Vegetation was sparse,

with cover only 12.0% along this transect, and consisted mostly of shrubs of *Styphelia tameiameia* (Epacridaceae) (Table 1), which rarely exceeded 0.5 m in height. Three endemic Hawaiian bunchgrasses, *Deschampsia nubigena*, *Trisetum glomeratum*, and *Agrostis sandwicensis*, were scattered (0.8–1.0% cover) components of the low vegetation. The endemic composite shrub *Dubautia menziesii* (Asteraceae) was locally common, but with only 0.5% total cover. *Tetramolopium humile* (Asteraceae), a small, mat-forming, locally endemic species, occurred (0.8% cover) only in these barren, high-elevation conditions. Only two alien herbaceous species were present: *Hypochoeris radicata* (Asteraceae) and *Rumex acetosella* (Polygonaceae), both sparse.

Transect 2 (2640–2660 m) passed through open shrubland with substantial (to 30% locally but only 11.5% total cover) cover of the native grass *Deschampsia nubigena* (Table 1). *Vaccinium reticulatum* (Ericaceae), *Coprosma montana* (Rubiaceae), *Styphelia tameiameia*, and *Sophora chrysophylla* (Fabaceae) were the dominant native shrubs, with total shrub cover ranging from 5 to 30% over the transect. The tallest of these, *Sophora*, rarely exceeded 3 m in height at this site. Alien plant species were rare here, with dicots *Hypochoeris radicata* and *Rumex acetosella* and monocots *Holcus lanatus* and *Poa pratensis* composing less than 10% of total cover. The percentage of bare ground was high (55.1%).

A slightly higher native species richness occurred at transect 3 (2430–2450 m) than at transects 1 and 2 (Table 1). *Styphelia* and *Vaccinium* were the dominant native shrubs, with cover estimates of 24.0 and 16.0%, respectively. This was the only site sampled where the relatively rare endemic species *Santalum haleakalae* (Santalaceae) and *Geranium cuneatum* (Geraniaceae) exceeded 1% of the cover (2 and 6%, respectively). *Santalum*, a small tree, ranged from 3 to 4 m in height, forming small, scattered groves; *Geranium*, a shrub, ranged up to 0.5 m in height. Cover of alien grass species, dominated by *Holcus*, rarely exceeded 15% locally. Bare ground covered 26.6% along this transect.

TABLE 1

ESTIMATED MEAN PERCENTAGE COVER ( $\pm$  SE) OF PLANT SPECIES ON FOUR ELEVATIONAL TRANSECTS LOCATED ON THE WESTERN AND NORTHWESTERN SLOPES ON HALEAKALĀ NATIONAL PARK

SPECIES	TRANSECT 1 (2860–2900 m)	TRANSECT 2 (2640–2660 m)	TRANSECT 3 (2430–2450 m)	TRANSECT 4 (2070–2130 m)
Native dicots				
<i>Styphelia tameiameia</i>	6.2 $\pm$ 2.4	3.0 $\pm$ 2.3	24.0 $\pm$ 5.6	31.2 $\pm$ 3.1
<i>Vaccinium reticulatum</i>	0.3 $\pm$ 0.3	6.2 $\pm$ 3.1	16.0 $\pm$ 4.3	13.8 $\pm$ 3.1
<i>Sophora chrysophylla</i>	—	2.8 $\pm$ 2.4	3.4 $\pm$ 1.9	9.0 $\pm$ 5.4
<i>Coprosma montana</i>	—	5.0 $\pm$ 2.0	4.2 $\pm$ 0.8	1.8 $\pm$ 1.1
<i>Coprosma ernodeoides</i>	—	—	0.6 $\pm$ 0.2	0.8 $\pm$ 0.3
<i>Dubautia menziesii</i>	0.5 $\pm$ 0.3	0.3 $\pm$ 0.3	0.6 $\pm$ 0.2	—
<i>Santalum haleakalae</i>	—	—	2.0 $\pm$ 2.0	+
<i>Geranium cuneatum</i>	—	0.5 $\pm$ 0.3	6.0 $\pm$ 1.0	—
<i>Tetramolopium humile</i>	0.8 $\pm$ 0.3	—	—	—
Alien dicots				
<i>Hypochoeris radicata</i>	1.0 $\pm$ 0.0	4.0 $\pm$ 1.0	1.0 $\pm$ 0.0	2.0 $\pm$ 1.0
<i>Rumex acetosella</i>	0.3 $\pm$ 0.3	1.0 $\pm$ 0.0	1.0 $\pm$ 0.0	—
<i>Danthonia pilosa</i>	—	—	0.4 $\pm$ 0.2	1.8 $\pm$ 1.1
Native monocots				
<i>Deschampsia nubigena</i>	1.0 $\pm$ 0.0	11.5 $\pm$ 6.4	1.0 $\pm$ 0.0	—
<i>Trisetum glomeratum</i>	0.8 $\pm$ 0.3	1.0 $\pm$ 0.0	1.0 $\pm$ 0.0	0.5 $\pm$ 0.3
<i>Agrostis sandwicensis</i>	1.0 $\pm$ 0.0	—	—	—
<i>Carex wahuensis</i>	—	+	1.0 $\pm$ 0.0	0.5 $\pm$ 0.3
<i>Luzula hawaiiensis</i>	—	0.3 $\pm$ 0.3	0.8 $\pm$ 0.2	0.3 $\pm$ 0.3
Alien monocots				
<i>Holcus lanatus</i>	—	2.5 $\pm$ 1.4	8.0 $\pm$ 1.2	8.8 $\pm$ 2.4
<i>Anthoxanthum odoratum</i>	—	—	1.0 $\pm$ 0.0	7.8 $\pm$ 3.0
<i>Poa pratensis</i>	—	2.0 $\pm$ 1.0	0.4 $\pm$ 0.2	—
Native fern				
<i>Pteridium aquilinum</i>	—	5.0 $\pm$ 0.0	1.0 $\pm$ 0.0	4.0 $\pm$ 1.0
Total vegetation	12.0	44.9	73.4	82.2
Bare ground and litter	88.3	55.1	26.6	17.8

Note: Percentage cover is based on estimates from four 10 by 10 m quadrats per transect. A species is included in the table if its mean cover value exceeded 0.5% on at least one transect. Species observed near but not in the sample plots are indicated by +.

The cover of native shrubs (56.6%) on transect 4 (2070–2130 m) was similar to that in transect 3 (Table 1). *Styphelia* was the dominant shrub, with *Vaccinium* and *Sophora* very common. This transect also had the highest mean cover of alien plant species (20.4%), with cover of introduced grasses (primarily *Holcus lanatus* and *Anthoxanthum odoratum*) ranging from 5% to 35% locally. The endemic grass *Deschampsia nubigena* was not recorded on this transect, and other native monocots were uncommon. Total vegetation cover approached 100% in places. On average, bare ground composed only 17.8% along the transect.

### Phenology of Vegetation

Phenology within the high-elevation shrubland of Haleakalā Volcano exhibits subtle year-to-year variations (L.L.L., unpubl. data) (Figure 2). Maximum vegetative growth for most plant species occurs during the months of March–June, at the end of the rainy season when soil moisture is generally high, temperatures are warming, and day length is increasing. Most, if not all, native species appear to have a dormant period, usually winter, when little or no vegetative growth occurs. Some alien species (e.g., *Hypochoeris radicata*, *Rumex acetosella*) may produce

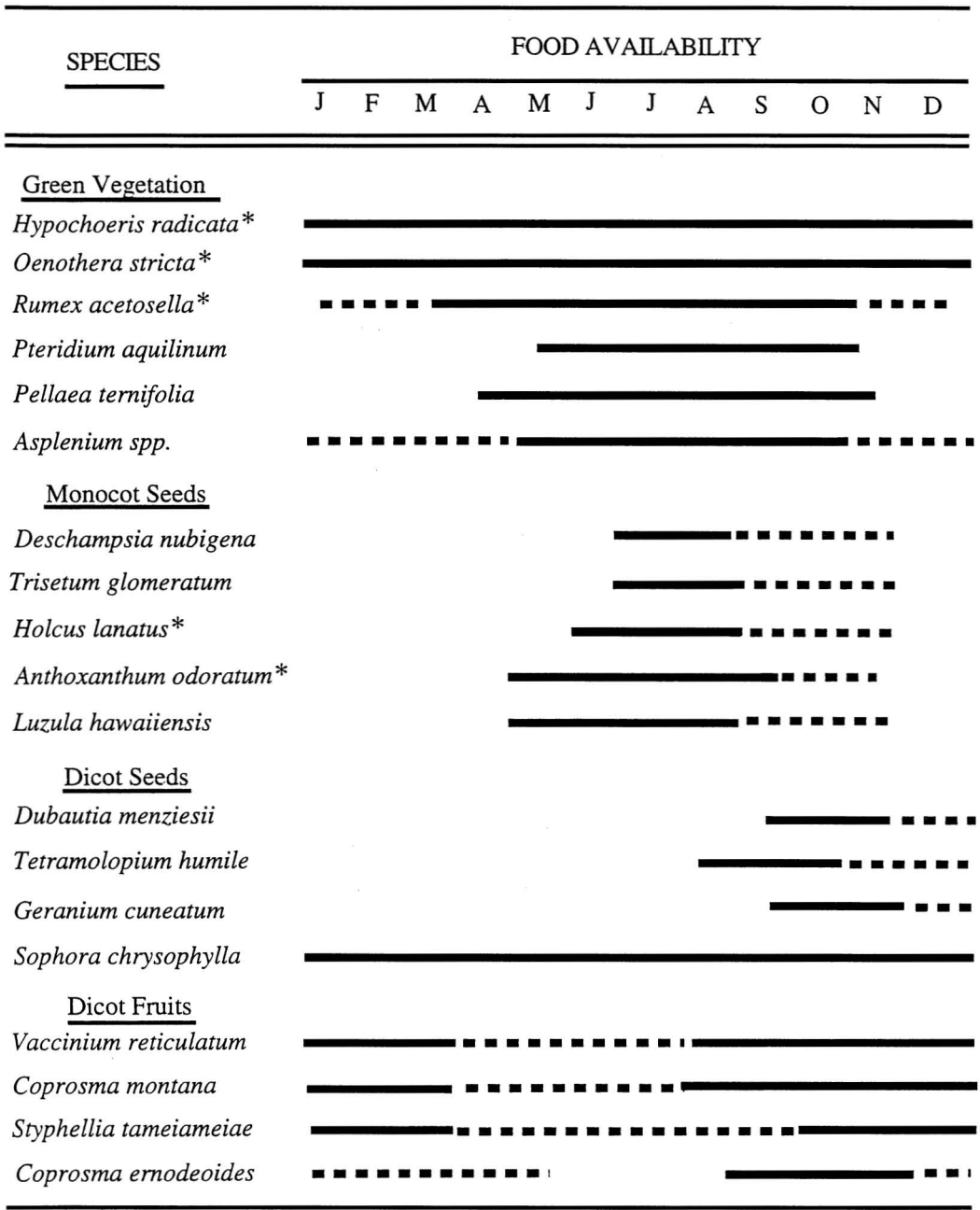


FIGURE 2. Monthly patterns of phenology for selected plant species that were found in the diets of *Mus musculus* and *Rattus rattus* living in the high-elevation shrubland of Haleakalā National Park. Solid bars indicate periods of general availability throughout the study area, and dashed bars indicate periods of only localized availability. Alien species are indicated by an asterisk.

leaves continuously throughout the year if soil moisture is adequate.

Both native and alien species have definite peak periods of flowering and fruiting, although almost any species may flower occasionally at any time of the year. Both native and alien grasses typically flower in May–June and set seed in July–September (Figure 2). Native shrubs flower sequentially. *Styphelia tameiameia* has a flowering peak in February–March; *Sophora chrysophylla* in March–April; *Vaccinium reticulatum*, *Coprosma montana*, and *C. ernodeoides* in May–June; *Geranium cuneatum* in August–September; and *Dubautia menziesii* in September–October. Peak production of ripe fruits by native shrubs occurs near the beginning of the November–April rainy season. Although many fruits fall to the ground after ripening, mature fruits of common native shrubs (e.g., *Styphelia tameiameia*, *V. reticulatum*, and *Coprosma*) may remain on the plants for many months.

#### Rodent Food Habits

Individual diet selection varied widely throughout the study depending on local availability of food items; some stomach samples were dominated by only one or two food types and others contained a variety of food items. Approximately 50% of the plant components of the *Mus musculus* diet were identifiable as food fragments from native (44.8%) or alien (5.3%) plant species. Alien plant species were taken most frequently by *Mus musculus* at the lowest elevation studied where alien species were common. Approximately 75% of plant components of the *Rattus rattus* diet were identifiable as food fragments from native (58.3%) or alien (17.3%) plant species. *Hypochoeris* leaves dominated the alien plant component of the *Rattus rattus* diet. Native arthropod species (e.g., representatives of Araneida, Hemiptera, Lepidoptera, and Coleoptera) were taken by both rodent species. Approximately 70% of the identifiable arthropod component of the composite *Mus musculus* diet was composed of Lepidoptera larvae (probably native species); slightly more than 25% of the identi-

able arthropod component of the composite *Rattus rattus* diet was composed of Lepidoptera larvae. Alien arthropod taxa (e.g., representatives of Isopoda, Dermaptera, and Homoptera) were also taken by *Mus musculus* and *Rattus rattus*.

A composite of the *Mus musculus* ( $n = 147$ ) and *Rattus rattus* ( $n = 29$ ) diets for animals living in the high-elevation shrubland was determined by combining data from animals collected on all transects during all sample periods. Over 75% of the composite *Mus musculus* diet was composed of arthropods, monocot seeds, and dicot seeds (Table 2). Arthropods (mostly adult and larval forms of ground-dwelling species) were more than twice as common in the *Mus musculus* diet as in the *Rattus rattus* diet when averaged over all months and elevations. *Mus musculus* ate large quantities of the seeds of both native (*Luzula hawaiiensis*, *Trisetum glomeratum*, *Deschampsia nubigena*) and alien (*Holcus lanatus*, *Anthoxanthum odoratum*) graminoids. They also took seeds of the common native shrubs (*Coprosma montana*, *C. ernodeoides*, *Vaccinium reticulatum*, *Styphelia tameiameia*, *Sophora chrysophylla*, and *Dubautia menziesii*). Adult *Mus musculus* took more arthropod material ( $36.9 \pm 3.1\%$  versus  $20.0 \pm 3.8\%$  [ $t = 2.999$ ,  $df = 145$ ,  $P = 0.003$ ]) and fewer monocot seeds ( $21.6 \pm 3.1\%$  versus  $34.4 \pm 4.9\%$  [ $t = 2.142$ ,  $df = 145$ ,  $P < 0.03$ ]) than juvenile animals. No differences in diets were observed between male and female *Mus musculus*.

In contrast to *Mus musculus*, monocot seeds and dicot seeds were only small components of the composite *Rattus rattus* diet (Table 2). Although dicot fruits composed slightly less than one-half of the *Rattus rattus* diet, dicot seeds made up <5% of their diet, suggesting that they were eating the fruit pulp more frequently than the seeds. *Rattus rattus* consumed particularly large quantities of the fruits of the native shrubs *Coprosma montana* and *Vaccinium reticulatum* and leaves of the alien herb *Hypochoeris radicata*, which were available throughout the year. Approximately 15% of the *Rattus rattus* diet was composed of arthropod material; juveniles took almost four times more arthro-



TABLE 2

MEAN ( $\pm$  SE) PERCENTAGE COMPOSITION OF DIFFERENT ITEMS IN THE COMPOSITE DIETS OF *Mus musculus* AND *Rattus rattus* FROM THE WESTERN AND NORTHWESTERN SLOPES OF HALEAKALĀ NATIONAL PARK

DIET ITEM	<i>Mus musculus</i> (147)	<i>Rattus rattus</i> (29)
Dicot seed	18.5 $\pm$ 2.0*	4.1 $\pm$ 1.2
Dicot fruit	10.1 $\pm$ 1.3	43.5 $\pm$ 6.2*
Dicot leaf	7.1 $\pm$ 1.1	20.6 $\pm$ 4.6*
Monocot seed	24.9 $\pm$ 2.6*	2.4 $\pm$ 0.9
Monocot leaf	0.7 $\pm$ 0.3	2.6 $\pm$ 1.3*
Arthropod	32.5 $\pm$ 2.6*	16.4 $\pm$ 3.5
Fern	2.8 $\pm$ 0.8	2.2 $\pm$ 0.8
Other	3.4 $\pm$ 0.5	5.8 $\pm$ 2.4

Note: Animals were collected during November 1984 and February, May, and August 1985 at four different elevations (2860–2900 m, 2640–2660 m, 2430–2450 m, and 2070–2130 m). Data represent the percentage composition of the diet fragments analyzed per stomach. Sample sizes are given in parentheses. Statistical difference ( $P < 0.05$ ) determined by *t*-test is indicated by an asterisk.

Pods than adults (22.9  $\pm$  4.5% versus 6.4  $\pm$  3.7% [ $t = 2.77$ ,  $df = 20$ ,  $P = 0.01$ ]). Monocot leaves and fern fronds were minor components of both diets.

Arthropods were important items in the diet of *Mus musculus* throughout the year, increasing in representation from late fall, through the winter, to early summer, and then declining by late summer (Figure 3). Although the arthropod component of the composite *Rattus* diet was approximately 50% smaller than for *Mus musculus*, arthropod composition in the *Rattus* diet showed a similar seasonal pattern. Maximum utilization of arthropods by *Mus musculus* and *Rattus* (56.2  $\pm$  5.0% and 26.3  $\pm$  5.4% of the diet, respectively) was in May, when both larvae and adults of many insect species were most abundant. Heavy consumption of arthropods by *Mus musculus* also occurred in February (36.5  $\pm$  4.6%) when grass seeds were scarce. Monocot seeds were readily available in the late summer to late fall but relatively scarce in late winter and spring. They dominated the *Mus musculus* diet in late summer, were still major diet items in November, and then declined in importance by February and May (Figure 3). Monocot

seeds were generally not taken by *Rattus rattus*. Dicot seeds, also commonly available in the late fall, were important *Mus musculus* food items in November and February; dicot seeds were most common in the *Rattus rattus* diet in November (8.3%). Fruits of the native shrubs were most frequently taken by *Mus musculus* in May (17.3%), but were only minor components of its diet at other times. Dicot fruits dominated the *Rattus rattus* diet in all but the May samples and composed 65.1% of the diet in August and more than 60% in November (Figure 3). Dicot leaves, stems, and flower parts were more important in the diet of *Rattus rattus* than in *Mus musculus* throughout the year, but were taken in a roughly similar seasonal pattern by both species. These diet items were most commonly taken in February and May by both species, with the *Rattus rattus* diet containing approximately four to five times more dicot leaves, stems, and flower parts than the *Mus musculus* diet.

The *Mus musculus* regime shows strong elevational as well as seasonal trends (Figure 4). Arthropods were important diet components at all elevations, during at least part of the year. Arthropods dominated the mouse diet at the highest elevation (transect 1) throughout the year, ranging in abundance from 27.8 to 74.9% of the diet. The highest percentage use of arthropods (74.9%) for any sampling date and location was recorded for this elevation in February, when alternative food items were extremely scarce. Ground-dwelling arthropods were a very common diet item in May and composed over 60% of the *Mus musculus* diet on transect 2 and transect 3 and 45% on transect 4 (Figure 4). Dicot seeds (with peak ripening in October–December) were important diet items at all elevations in November and February. Their importance in the diet increased by twofold between the highest (transect 1) and lowest (transect 4) sites. Fern fronds, usually a minor diet component at all elevations, made up 20% of the *Mus musculus* diet on transect 3 in February, when alternative foods may have been scarce locally. Grass seeds were most important in the *Mus musculus* diet at all elevations in August. They were taken in

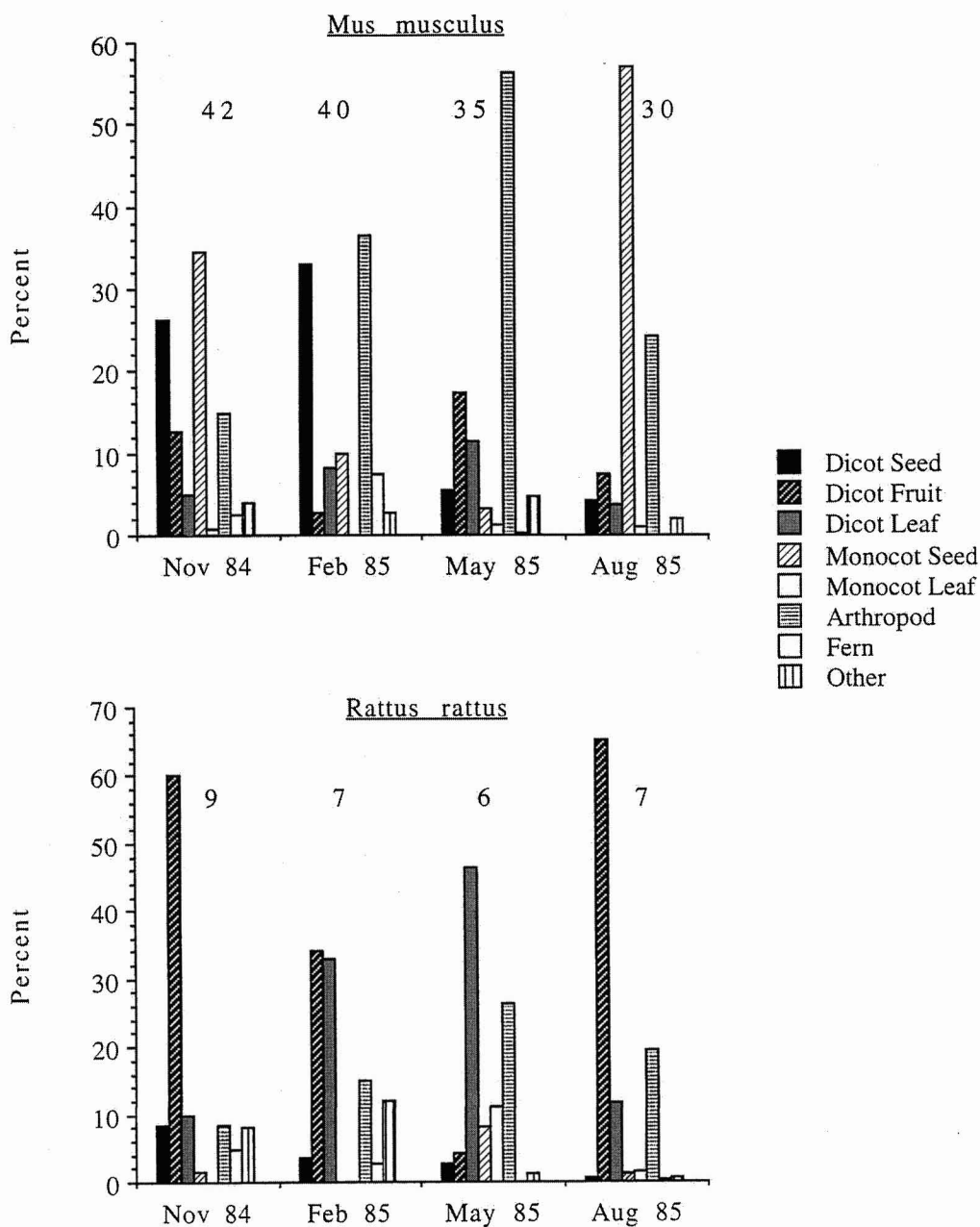


FIGURE 3. Seasonal changes in diet composition for *Mus musculus* and *Rattus rattus* on the western and north-western slopes of Haleakalā Volcano. Animals were collected during November 1984 and February, May, and August 1985. Data represent the percentage composition of the diet item in the total fragments analyzed per stomach. Sample sizes are given above the bars for each date.

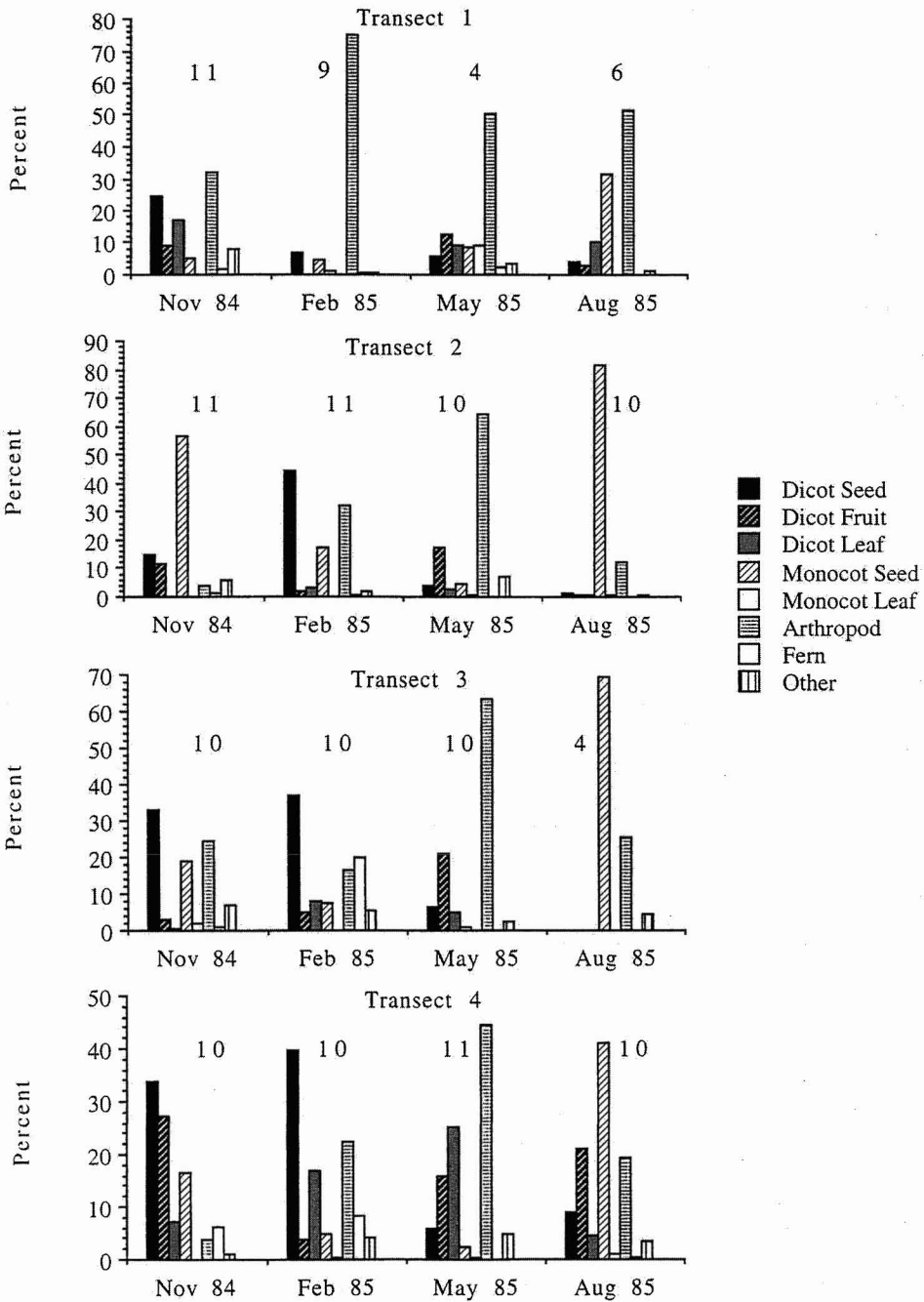


FIGURE 4. Seasonal changes in diet composition for *Mus musculus* living at four elevations (2860–2900 m [T1], 2640–2660 m [T2], 2430–2450 m [T3], and 2070–2130 m [T4]) on the western slope of Haleakalā Volcano. Animals were collected during November 1984 and February, May, and August 1985. Data presented represent the percentage composition of the diet item in the total fragments analyzed per stomach. Sample sizes for each date are given above the bars.

TABLE 3

PERCENTAGE OF *Mus musculus* AND *Rattus rattus* STOMACHS THAT CONTAINED IDENTIFIABLE MATERIAL FROM SPECIFIC ARTHROPOD TAXA

TAXA	NOV. 1984		FEB. 1985		MAY 1985		AUG. 1985	
	<i>Mus</i> (42)	<i>Rattus</i> (9)	<i>Mus</i> (58)	<i>Rattus</i> (7)	<i>Mus</i> (43)	<i>Rattus</i> (6)	<i>Mus</i> (30)	<i>Rattus</i> (7)
Araneida	68.8	25.0	50.0	87.5	39.5	40.0	30.0	14.3
Theridiidae	28.1	12.5	24.1	12.5	14.0	0	3.3	0
Lycosidae	6.3	0	8.6	25.0	0	0	3.3	0
Chilopoda	9.4	12.5	10.3	12.5	2.3	0	6.7	0
Isopoda	15.6	12.5	22.4	0	14.0	0	20.0	0
Dermaptera	6.3	12.5	5.2	62.5	0	0	0	0
Homoptera	50.0	12.5	41.4	25.0	4.7	0	0	0
Aphidae	28.1	12.5	10.3	12.5	14.0	0	10.0	0
Delphacidae	18.8	0	12.1	25.0	2.3	0	0	0
Pseudococcidae	12.5	0	22.4	12.5	18.6	0	3.3	14.3
Hemiptera	15.6	12.5	31.0	50.0	9.3	20.0	3.3	0
Nabidae	12.5	0	29.3	37.5	16.3	0	10.0	0
Miridae	3.1	0	0	0	0	0	0	0
Lepidoptera								
Adults	6.3	37.5	6.9	25.0	27.9	0	10.0	14.3
Larvae	40.6	50.0	77.6	37.5	41.9	40.0	36.7	100.0
Diptera								
Adults	28.1	37.5	19.0	37.5	2.3	0	0	14.3
Larvae	12.5	12.5	0	0	14.0	20.0	0	0
Hymenoptera	15.6	0	13.8	37.5	25.6	60.0	3.3	14.3
Coleoptera								
Adults	9.4	87.5	15.5	62.5	4.7	0	0	14.3
Larvae	3.1	0	5.2	12.5	0	0	0	0
Curculionidae	9.4	75.0	12.1	25.0	4.7	0	0	0
Carabidae								
Adults	0	37.5	1.7	3	2	0	40.0	0
Larvae	0	0	3.4	0	0	0	0	0

Note: Animals were collected on the western and northwestern slopes of Haleakalā Volcano during November 1984, February 1985, May 1985, and August 1985. Sample sizes are given in parentheses.

greatest numbers on transects where grasses locally dominated the vegetation cover and seeds were readily available. Grass seeds composed 83.6 and 66.5% of the mouse diet on transect 2 during August and November, respectively, and 69.5% of the August diet on transect 3. Dicot leaves were taken in the highest proportions at transect 4, but were not common diet items at any elevation. Too few *Rattus rattus* were captured to determine elevational variation in diet selection.

Both rodent species took a variety of arthropod taxa as food items, especially

Araneida, Homoptera, Hemiptera, and the adults and larvae of Diptera, Coleoptera, and Lepidoptera (Table 3). These taxa include many endemic species and the most abundant ground-dwelling arthropods in the study area. Arthropods composed a larger percentage of the rodent diet at high elevation due to the general scarcity of plant foods at this location (Figure 4). Native Lepidoptera larvae of the genus *Agrotis*, lycosid spiders, and curculionid and carabid beetles dominated the arthropod component of the rodent diets at high elevation (transect 1).

Lepidoptera larvae, alien Isopoda and Dermaptera, and Homoptera were commonly taken at lower elevations.

## DISCUSSION

### *Rodent Food Habits*

*Mus musculus* and *Rattus rattus* are opportunistic omnivores that feed on a variety of plant and arthropod tissue (Kami 1966, Daniel 1973, Clark 1982, Sugihara 1997). Both species also are cannibalistic at times. Plant material dominated the diets of both species during most seasons, with the notable exception of *Mus musculus* at the highest elevations (Figures 3 and 4). Arthropod foods were most important in the May diet when fruits and seeds were uncommon. Seasonal differences in availability of plant foods were also reflected in the diet selection by both species (Figure 3). Dicot fruits are important food items for both species during the fall and early winter when they are readily available. Monocot seeds, a major component of the *Mus musculus* diet in late summer to early winter and a good source of energy, were only minor components of the *Rattus rattus* diet, probably because of their small size and the difficulty in handling them. Arthropods were important food items for *Mus musculus* throughout the study, but particularly in the winter and spring when alternative foods were scarce. During the winter and spring, adult *Rattus rattus* took considerably more green foliage, primarily alien dicots (especially *Hypochoeris radicata*) common throughout the study area, and less arthropod material than *Mus musculus*. Perhaps this difference in diet selection is a reflection of the greater energy or protein content of arthropod prey versus plant prey and the higher energetic costs of living in the severe microclimate typical of the western slope of Haleakalā Volcano, especially near the summit for the smaller-bodied *Mus musculus* versus the larger-bodied *Rattus rattus*. Arthropods are often taken in larger proportions by juvenile rodents (Clark 1982,

Sugihara 1997) or immature game birds (Cole et al. 1995) than by adults because of their high energetic and protein contents and the need to meet the physiological demands of rapid growth at this age. This pattern was followed by *Rattus rattus* in this study, but *Mus musculus* adults took significantly more arthropods than juveniles; juvenile *Mus musculus* took a significantly larger proportion of monocot seeds, which are also a good source of energy, but a food resource that is distributed in patches and may not require extended foraging periods to exploit.

The *Mus musculus* diet reflects changes in the relative abundance of specific prey items with increasing elevation (Figure 4, Table 1). Dicot fruits decrease in importance in the *Mus musculus* diet as elevation increases because shrubs are less common and grasses more abundant at higher elevations. Monocot seeds are important components of the late summer diet (August) at all elevations, but exceed 68% of the diet at transect 3 and 78% of the diet at transect 2, elevations where grass abundance is high. Arthropod material, particularly ground-dwelling Lepidoptera larvae, Araneida, and flightless Coleoptera, increased in importance in the *Mus musculus* diet with increasing elevation and decreasing availability of alternative food items. Highly digestible plant material is not abundant in any season at the highest elevation, where bare ground and rock approximate 90% of the coverage. Arthropods composed large proportions of the *Mus musculus* diet throughout the year at this elevation, but particularly in winter (75% of the diet), when plant food items were most scarce. In May, when fruits and seeds were relatively scarce, arthropod material dominated the *Mus musculus* diet at all elevations.

Although primarily opportunistic feeders, both *Mus musculus* and *Rattus rattus* differentially selected some food items over others during specific seasons or at specific elevations. Especially at the highest elevations, *Mus musculus* took arthropod prey (e.g., Lepidoptera larvae [probably native species], native Araneida, and native Coleoptera adults) more frequently than would have

been predicted from availabilities projected from extensive pitfall trapping in the area (Cole et al. 1992). Dicot fruits and leaves (other than tough, probably difficult to digest *Styphelia* leaves) in November and native monocot seeds in August appear to have been taken disproportionately to their general abundance in the study area. Although *Styphelia* was the most common native shrub at lower elevations, fruits of *Vaccinium* and *Coprosma* dominated the dicot fruit component of the *Mus musculus* diet, probably reflecting the greater amount of pulp available in these fruits versus those of *Styphelia*. *Rattus rattus* took dicot fruits (especially *Vaccinium* and *Coprosma* fruits) and dicot leaves (especially *Hypochoeris radicata* leaves) in greater frequency than was predicted from their general availability in the area.

In general, the foods selected by both species tended to be of high nutritional quality. Important plant foods were fruits, which are high in digestible carbohydrates, and dicot and monocot seeds, which are often high in protein and fats. Fruits dominated the *Rattus rattus* diets and seeds dominated the *Mus musculus* diets in most seasons. Animal foods are sources of balanced protein and energy for both species and were present in most stomachs analyzed for every sample period (88% of all *Mus musculus* and 80% of all *Rattus rattus* stomachs). Food quality may influence strongly the reproductive success of both species (Clark 1981). Less-nutritious plant foods such as dicot stems and monocot leaves were not heavily taken by either species; *Rattus rattus* did take what appeared to be readily digestible dicot leaves (especially *Hypochoeris radicata*) in winter and spring when alternative foods were uncommon, possibly as a source of water. This pattern of selecting high-quality foods has been reported for *Rattus rattus* in several studies (see Clark 1981).

#### *Impact of Introduced Rodents on the Endemic Biota of Upper Haleakalā*

The potential for damage to plant populations by *Rattus rattus* in the Galápagos Islands has been noted by Clark (1981), who

found that rats are primarily herbivorous, prefer reproductive structures of plants, destroy nearly all seeds ingested, and often concentrate on relatively uncommon species. Similar concerns apply to many Hawaiian habitats (e.g., Baker 1979, Scowcroft and Sakai 1984). In high-elevation shrubland, a plant species very likely to be affected is the relatively rare Haleakalā sandalwood, *Santalum haleakalae*. Mature sandalwood fruits are uncommon, and seedlings are almost never seen. Rodent-gnawed seed casings are commonly found under sandalwood trees. Another very rare tree of the high-elevation shrubland, *Pittosporum confertiflorum*, is also likely to be affected by rats. However, our (A.C.M., L.L.L.) field observations for two decades suggest that most native plant species encountered in this study have fairly stable populations and are not substantially affected in the short term by rodent predation.

Intact seeds of several food plants, particularly *Vaccinium*, were visible in rodent droppings. Although native shrub and alien grass seeds have germinated from game bird droppings under similar conditions (Cole et al. 1995), no germination was obtained from the greenhouse flats sown with rodent fecal material (F.R.C., unpubl. data).

Particularly on islands, *Rattus rattus* has been shown to reduce bird populations (Atkinson 1977, 1985) and arthropod populations (Best 1969, Clark 1980). In the high-elevation shrubland of Haleakalā, *Rattus rattus* is not generally believed to be a major predator on either the Dark-rumped Petrel (Simons 1985) or the Nēnē (Banko and Manuwal 1982). As in rain forest habitats, *Rattus rattus* and *Mus musculus* may be more influential as prey for mongooses, feral cats, and raptors than as avian predators (Sugihara 1997).

*Rattus rattus* and *Mus musculus* are important consumers of invertebrates and take a wide variety of native species. On upper Haleakalā, we believe that *Mus musculus* may have dramatic negative effects on locally endemic arthropods, particularly during periods of high density. Although *Mus musculus* numbers were modest at the 2860–2900 m elevation transect (F.R.C., L.L.L., A.C.M.,

unpubl. data), where vegetation and invertebrate life were sparse, arthropods composed approximately 33–75% of the mouse diet throughout the year. In February, when plant food was scarce near the summit, three-fourths of the *Mus musculus* diet was composed of arthropods, most of which were endemic. About 35% of the *Mus musculus* diet pooled over all elevations was composed of invertebrates versus about 15% invertebrates in the *Rattus rattus* diet. Lepidoptera larvae, including probable native pollinator species of native shrubs, are common diet items for both species. Both rodent species are also sharply reducing populations of the endemic, ground-dwelling arthropods of Haleakalā, many of which are rare, very locally endemic, and/or flightless (Beardsley 1980, Medeiros and Loope 1994). *Mus musculus* appears to have a greater potential to deplete the endemic arthropod biota than *Rattus rattus* because of its greater abundance, especially in the fall (F.R.C., L.L.L., A.C.M., unpubl. data), and its apparent ability for finding and feeding on arthropod larvae and adults when other potential food items are scarce.

In conclusion, both rodent species exert predation pressure on local arthropod populations, including those of endemic species. *Mus musculus* populations may have more impact because of their greater abundance, especially in the fall. Rodent exclusion studies might allow assessment of the magnitude of impacts of rats and mice on populations of native arthropods. Such studies might be particularly feasible and meaningful near the summit of Haleakalā Volcano because of relatively low rodent population levels (using newly developed and evolving control methods) and the relative absence of other alien influences on the endemic arthropod fauna (potential for vigorous response).

#### ACKNOWLEDGMENTS

The Entomology Department of the B. P. Bishop Museum in Honolulu provided work space to F.R.C. during a sabbatical leave. The advice and encouragement from mu-

seum entomologists Wayne Gagné, Frank Howarth, Alan Samuelson, Neil Evenhuis, and Gordon Nishida as well as other members of the department were greatly appreciated. C. Crivellone, D. Rasfeld, P. Rasfeld, R. Richardson, and K. Schlom helped with rodent trapping. A. Lamontagne, T. McAllister, and T. Shyka assisted with laboratory work and data analysis.

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