

Abundance and Diets of Rats in Two Native Hawaiian Forests¹

ROBERT T. SUGIHARA²

ABSTRACT: Snap traps were set and monitored in two native Hawaiian rain forests on Maui, Hawai'i, to determine the relative abundances, distributions, and diets of rodents. Black rats (*R. rattus*), Polynesian rats (*R. exulans*), and mice (*Mus musculus*) were abundant throughout the mesic to wet forest habitat in both areas from 1600 to 2000 m elevation during both summer and winter trapping periods. Invertebrates, particularly insect larvae, were the most frequently found and abundant food item in the stomachs of both rat species. Consumption of these prey by rats was higher in winter than in summer. Black rats ate more fruits, seeds, and other vegetation than did Polynesian rats. More information about the life history, ecology, and behavior of rats in native Hawaiian forests is needed to document their impact on endemic ecosystems and to develop effective control techniques.

COLONIZATION BY HUMANS has resulted in the introduction of rats (*Rattus* spp.) and mice [*Mus musculus* (L.)] to most major islands in the Pacific Ocean, and today these rodents cause a myriad of economic, health, and ecological problems throughout the region (Atkinson 1985, 1989, Tomich 1986, Buckle and Fenn 1992, Moors et al. 1992). Ecological disruptions have been particularly devastating to insular communities with flora and fauna that evolved in the absence of predators.

Polynesian rats [*Rattus exulans* (Peale)] accompanying early Polynesian settlers arrived in Hawai'i about 1600 yr ago (Kirch 1982). Norway rats [*R. norvegicus* (Berkenhout)] reached the Islands shortly after the arrival of Captain James Cook in 1778. House mice followed soon after, but roof rats [*R. rattus* (L.)] probably did not reach Hawai'i until after 1870 (Tomich 1986). All three rat species have been implicated in the decline of threatened and endangered plants (Baker and Allen 1976, Russell 1980, Scowcroft and Sakai 1984, Stone 1985), snails (Hadfield et al. 1993), and birds (Kepler 1967, Fleet 1972, Buxbaum 1973, Atkinson 1977,

Berger 1981, Simons 1983, Tomich 1986) in Hawai'i.

Loss and destruction of habitat by humans, disease, and competition from introduced plants and animals have virtually eliminated many of Hawai'i's endemic biota from the lowlands and middle-elevation areas. Most extant native species, especially forest birds, now survive in relatively low numbers in restricted areas of high-elevation remnant rain forests (Scott et al. 1986). Current information on rodent populations and their role as potential predators in these native forests is lacking and could shed insight on the conservation of Hawai'i's endemic resources. Thus, I determined the relative abundance and diets of black and Polynesian rats during the wet (winter) and dry (summer) periods in two relatively undisturbed upper-elevation Hawaiian rain forests.

MATERIALS AND METHODS

Study Area

The study was conducted in two montane rain forest preserves on the northeastern slope of Haleakalā on the island of Maui, Hawai'i (Figure 1): the 3035-ha Hanawā Natural Area Reserve (HNAR) and the 2100-ha Waikamoi Nature Preserve (WNP). The two preserves contain most of the last remnant populations of four endangered bird species.

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² Denver Wildlife Research Center, U.S. Department of Agriculture, P.O. Box 10880, Hilo, Hawai'i 96721.

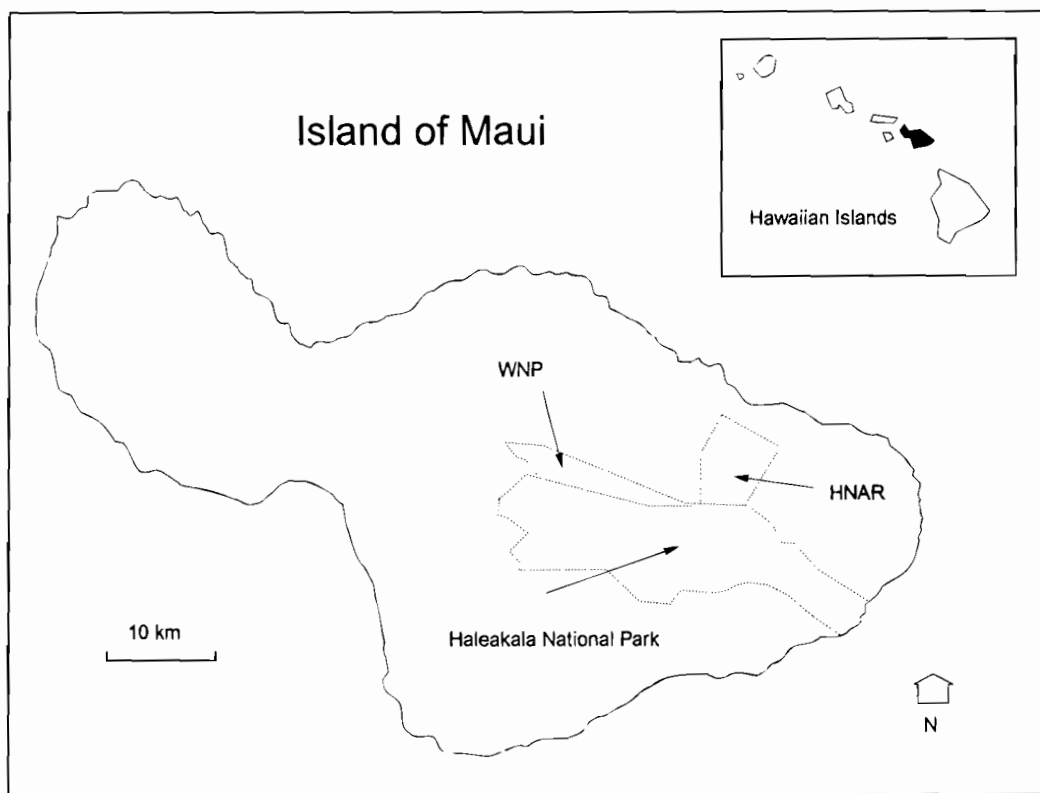


FIGURE 1. Boundaries of Waikamoi Nature Preserve (WNP) and Hanawi Natural Area Reserve (HNAR) adjacent to Haleakala National Park on the island of Maui, Hawai'i.

The HNAR site included 100 ha between the east and west forks of Hanawi stream, extended from 1505 to 2125 m elevation, and contained moderately sloping to steep terrain with well-to poorly drained organic soil. Mean annual precipitation varies from 250 to >500 cm. Above 2100 m, the area consisted of mesic-zone subalpine scrub vegetation (*Styphelia* spp., *Vaccinium* spp., *Coprosma* spp., and *Rubus* spp.), ground ferns (*Sadleria* spp.), and scattered patches of alpine grasses (*Deschampsia* spp. and *Holcus* spp.). A narrow mesic band of 'ohi'a (*Metrosideros polymorpha*) extended from 2000 to 2100 m and merged into wetter 'ohi'a forest at the lower limits (1500–2000 m). Other trees and shrubs in the lower 'ohi'a zone included *Cheirodendron* spp., *Pelea* spp., *Myrsine* spp., *Pitosporum* spp., the epiphyte *Astelia* spp., and rare and endangered specimens of *Cyanea* spp. and *Cleramontia* spp. Native ferns (*Dryopteris*

spp. and *Athyrium* spp.) dominated the ground cover. Between 1500 and 1600 m elevation, uprooting by feral pigs (*Sus scrofa*) destroyed much of the understory mosses, lichens, liverworts, *Stenogyne* spp., *Rubus* spp., and *Peperomia* spp., often resulting in eroded slopes, muddy wallows, and invasion of exotic plants.

The WNP site encompassed 300 ha of mesic-to wet-zone 'ohi'a and koa (*Acacia koa*)-'ohi'a forest and ranged from 1500 to 1850 m in elevation. The preserve receives about 375 cm of precipitation annually. The topography was more uniform, less rugged, and less steep than that in HNAR. The overstory canopy consisted of 'ohi'a and koa with subcanopy, shrub, and groundcover vegetation similar to that found in Hanawi. Ground ferns were more abundant than in HNAR. Extensive fencing and ungulate eradication programs mitigated disturbance of understory vegetation by pigs.

Rat Populations

Two transects were laid out in HNAR and three transects in WNP along previously established access trails. The transects in HNAR were 1525 m long, 450–600 m apart, and ran perpendicular (north-south) to the elevational contour. Those in WNP varied from 600 to 1245 m long and were 1000 m apart. Two transects in WNP followed the 1500-m and 1585-m contours, and a third extended from 1700 to 1850 m elevation. Transects in both preserves were located >8 km from established human habitation.

I set and checked standard rat snap traps for three consecutive nights during November–December 1985 (1128 trap nights), and May–June 1986 (1359 trap nights). Traps were secured with wire flags to the ground under vegetation or fallen logs at 15- to 20-m intervals along each transect and left in the same location for the three nights of trapping. I scattered grated coconut along each transect 2–3 days before setting the traps, which were baited with chunks of coconut. This bait is accepted by all rodent species in Hawai'i and is used routinely in trapping in a variety of different habitats (Tobin and Sugihara 1992). I checked the traps before 1000 hours each day and recorded the location, species, gender, body weight, and age (adult or juvenile) of each capture. I collected and labeled carcasses and rebaited and reset traps as necessary. All traps were removed between trapping sessions.

I used analyses of variance (ANOVA [SAS Institute 1988]) to detect differences in capture success, expressed as number of captures per 100 trap nights, among areas, trapping periods (summer/winter), and rat species. Duncan's multiple-range test with $P < 0.05$ (Saville 1990) was used to separate treatment and interaction means. I used Chi-square tests (SAS Institute 1988) to detect differences in rat capture success by age class for each period and species.

Diet Analysis

The stomach and 0.5–1.0 cm of the esophagus and intestine of each rat were removed and preserved in 70% ethyl alcohol on the day of capture. I later weighed the stomach, made an incision along the convex surface, peeled back the stomach wall, and rinsed the contents into a

beaker with 2% detergent solution. The contents were swirled in 50 ml of detergent solution for 5 min to separate the contents and dissolve gastric juices, stomach oils, and grease. Then the contents of the beaker were poured into a 35-mesh (0.4-mm opening) sieve and rinsed with tap water until the filtrate appeared clear. I examined the contents in a petri dish under a dissecting microscope at $10\times$ magnification, using a 1-cm² grid under the petri dish to help quantify the abundance of food items in each sample. I removed parasitic roundworms and discarded empty stomachs and samples that contained >50% by volume roundworms or coconut bait. Mice stomachs were not collected.

Stomach contents were classified into four major food types: invertebrates (arthropods, earthworms, slugs, and snails), fruits and seeds, other vegetation (leaves, stems, roots, rhizomes), and animal matter (rodent fur and flesh). I calculated the percentage occurrence of each food type as the percentage of stomachs in which the food type occurred. I used the "points method" described by Hynes (1950) to estimate the relative abundance of each food type. Based on size and frequency of items in each stomach, a score ranging from 0 to 5 (estimated proportion of individual contributions) was assigned to each food type as follows: 0 (absent), 1 (<0.5%), 2 (0.5–5%), 3 (>5 to 25%), 4 (>25 to 50%), and 5 (>50%). I calculated the relative abundance of each food type by dividing the sum of the scores for each food type for all rats by the sum of scores for all food types.

An ANOVA (SAS Institute 1988) was used to examine differences in percentage occurrence and relative abundance of major food types between areas, trapping periods, and rat species. I conducted another ANOVA combining observations for the two trapping periods to detect differences in diet of adult and juvenile rats between areas and species. Duncan's multiple-range test with $P < 0.05$ (Saville 1990) was used to separate treatment and interaction means.

RESULTS

Rat Populations

I captured 279 black rats, 158 Polynesian rats, 132 house mice, and one mongoose (*Herpestes*

TABLE 1

NUMBER OF CAPTURES PER 100 TRAP NIGHTS OF RATS AND MICE DURING NOVEMBER–DECEMBER 1985 (WINTER) AND MAY–JUNE 1986 (SUMMER) IN TWO NATIVE MONTANE RAIN FORESTS ON THE ISLAND OF MAUI, HAWAII

LOCATION	SPECIES	WINTER		SUMMER	
		MEAN	SEM	MEAN	SEM
HNAR	<i>R. rattus</i>	8.3	3.8	7.8	2.3
	<i>R. exulans</i>	6.5	0.1	6.4	1.1
	<i>M. musculus</i>	5.3	1.4	5.4	0.2
WNP	<i>R. rattus</i>	13.0	6.4	16.3	5.0
	<i>R. exulans</i>	4.2	0.7	7.8	0.9
	<i>M. musculus</i>	3.1	0.9	6.6	2.9

NOTE: Standard rat snap traps were set along two transects in Hanawā Natural Area Reserve (HNAR) and three transects in Waikamoi Nature Preserve (WNP).

auropunctatus) during 2479 trap nights. Capture success for black rats did not differ between areas ($F = 2.58$; $df = 1, 3$; $P = 0.20$) or sampling periods ($F = 0.04$; $df = 1, 3$; $P = 0.85$) (Table 1). Fewer Polynesian rats were captured at WNP during winter ($F = 14.64$; $df = 1, 3$; $P = 0.03$) than during summer or at HNAR during either period. Black rats were trapped throughout both study areas. Polynesian rats and mice were captured throughout WNP, but only above 1600 m elevation in HNAR, where disturbance by feral pigs was minimal.

Overall, the male to female ratio was 1.10 for black rats and 1.27 for Polynesian rats (Table 2). Juvenile rats composed 14–20% and 14–34% of captures for black and Polynesian rats, respec-

tively (Table 2). The percentage of Polynesian rat captures classed as juveniles was higher ($\chi^2 = 4.67$, $df = 1$, $P = 0.03$) in winter (33.3%) than during summer (13.6%) in HNAR (Table 2). I detected no differences between trapping periods in the percentage of captures that were juveniles for Polynesian rats in WNP (summer, 30.2%; winter, 38.9%; $\chi^2 = 0.46$, $df = 1$, $P = 0.49$) or for black rats in either HNAR (summer, 17.0%; winter, 15.4%; $\chi^2 = 0.05$, $df = 1$, $P = 0.82$) or WNP (summer, 19.4%; winter, 13.8%; $\chi^2 = 0.80$, $df = 1$, $P = 0.37$) (Table 2).

Mean adult body weight was higher in summer than in winter for both Polynesian ($F = 3.83$; $df = 1, 3$; $P = 0.05$) and black rats ($F = 20.26$; $df = 1, 3$; $P < 0.01$) (Table 2). Body weights of Polynesian rats ($F = 1.56$; $df = 1, 3$; $P = 0.30$) and black rats ($F = 0.17$; $df = 1, 3$; $P = 0.71$) were similar between forest locations. I captured pregnant rats only during the summer. Ten of 72 (13.9%) black rats and two of 44 (4.5%) Polynesian rats contained from four to eight mid- to almost full-term fetuses. I did not assess the reproductive condition of mice.

Diet

I examined 178 and 224 rat stomachs from HNAR and WNP, respectively. Invertebrates (mostly arthropods) were the most common food type in both rat species (Table 3). Insect larval fragments (predominantly Lepidoptera), chitinous fragments of adult arthropods, and other

TABLE 2

TOTAL CAPTURES (n), ADULT BODY WEIGHT, AND AGE-SEX STRUCTURE OF RATS TRAPPED DURING NOVEMBER–DECEMBER 1985 (WINTER) AND MAY–JUNE 1986 (SUMMER) IN TWO NATIVE MONTANE RAIN FORESTS ON THE ISLAND OF MAUI, HAWAII

		WINTER					SUMMER				
			ADULT BODY WT (g)		%			ADULT BODY WT (g)		%	
LOCATION	SPECIES	<i>n</i>	MEAN	SEM	YOUNG	MALES	<i>n</i>	MEAN	SEM	YOUNG	MALES
HNAR	<i>R. rattus</i>	53	149.1	3.4	15.4	51.9	53	163.1	4.5	17.0	49.1
	<i>R. exulans</i>	42	64.2	2.0	33.3	57.1	44	69.8	1.2	13.6	63.6
WNP	<i>R. rattus</i>	58	145.2	4.3	13.8	43.1	108	172.2	4.0	19.4	54.1
	<i>R. exulans</i>	18	70.1	3.9	38.9	61.1	53	72.5	1.5	30.2	47.2

NOTE: Standard rat snap traps were set along two transects in Hanawā Natural Area Reserve (HNAR) and three transects in Waikamoi Nature Preserve (WNP).

TABLE 3

PERCENTAGE OCCURRENCE AND MEAN RELATIVE ABUNDANCE (IN PARENTHESES) OF MAJOR FOOD TYPES IDENTIFIED IN STOMACHS OF RATS TRAPPED DURING NOVEMBER–DECEMBER 1985 (WINTER) AND MAY–JUNE 1986 (SUMMER) IN TWO NATIVE MONTANE RAIN FORESTS ON THE ISLAND OF MAUI, HAWAII

LOCATION	SEASON	SPECIES	<i>n</i>	INVERTEBRATES	FLESHY FRUITS	OTHER PLANT MATERIAL	RODENT FUR AND FLESH
HNAR	Winter	<i>R. rattus</i>	44	97 (42)	84 (53)	9 (2)	3 (2)
		<i>R. exulans</i>	40	98 (96)	8 (3)	2 (1)	0 (0)
	Summer	<i>R. rattus</i>	52	85 (38)	52 (33)	66 (28)	1 (1)
		<i>R. exulans</i>	42	92 (67)	23 (14)	45 (19)	0 (0)
WNP	Winter	<i>R. rattus</i>	58	98 (45)	42 (23)	40 (23)	23 (10)
		<i>R. exulans</i>	16	100 (93)	18 (3)	15 (4)	0 (0)
	Summer	<i>R. rattus</i>	98	88 (34)	65 (37)	64 (28)	5 (1)
		<i>R. exulans</i>	52	93 (76)	29 (16)	27 (8)	0 (0)

NOTE: Standard rat snap traps were set along two transects in Hanawā Natural Area Reserve (HNAR) and three transects in Waikamoi Nature Preserve (WNP).

nonrodent animal material (including snails, slugs, and earthworms) occurred in 85–100% of rat stomachs, with a mean relative abundance of 34–96% (Table 3). I found invertebrates in a greater proportion of stomachs ($F = 30.80$; $df = 1, 3$; $P = 0.01$) and with a greater relative abundance ($F = 83.36$; $df = 1, 3$; $P < 0.01$) during winter (98.5% occurrence, 68.7% abundance) than during summer (89.9% occurrence, 53.8% abundance). The percentage occurrence of invertebrates in stomachs of black (92.5%) and Polynesian (95.9%) rats was similar ($F = 1.74$; $df = 1, 3$; $P = 0.28$), although the relative abundance of that food type was greater ($F = 1101.2$; $df = 1, 3$; $P < 0.01$) for Polynesian rats (83.1%) than for black rats (39.5%) (Table 3). I found invertebrates in 92.7% of adults and 92.3% of juvenile rat stomachs ($F = 0.01$; $df = 1, 3$; $P = 0.93$), but in greater relative abundance ($F = 18.04$; $df = 1, 3$; $P = 0.02$) in juveniles (71.7%) than in adults (57.1%). Percentage occurrence ($F = 1.32$; $df = 1, 3$; $P = 0.33$) and relative abundance ($F = 0.09$; $df = 1, 3$; $P = 0.78$) of invertebrates in the diet of both rat species did not vary between HNAR (93.0% occurrence, 61.8% abundance) and WNP (95.0% occurrence, 60.6% abundance).

Black rats ate more fleshy fruits and seeds (*Rubus* spp., *Psittosporum* spp., and *Coprosma* spp.) than did Polynesian rats (occurrence: black rats, 59.4%; Polynesian rats, 20.3%; $F = 23.83$; $df = 1, 3$; $P = 0.02$; relative abundance: black rats, 35.1%; Polynesian rats, 9.5%; $F = 21.58$;

$df = 1, 3$; $P = 0.02$). Fruits and seeds were present in more adult stomachs (49.5%) ($F = 10.17$; $df = 1, 3$; $P = 0.05$) than juvenile stomachs (23.3%) but occurred in similar relative abundance ($F = 4.67$; $df = 1, 3$; $P = 0.12$) in both age classes (adults, 27.0%; juveniles, 14.8%). I did not detect any differences between trapping periods in consumption of fleshy fruits and seeds (percentage occurrence: winter, 36.3%; summer, 43.4%; $F = 0.27$; $df = 1, 3$; $P = 0.64$; relative abundance: winter, 19.2%; summer, 25.4%; $F = 1.04$; $df = 1, 3$; $P = 0.38$). Percentage occurrence (HNAR, 41.5%; WNP, 38.8%; $F = 0.05$; $df = 1, 3$; $P = 0.83$) and relative abundance (HNAR, 26.1%; WNP, 19.8%; $F = 1.19$; $df = 1, 3$; $P = 0.35$) of that food type were also similar between areas.

Fragments of leaves, stems, roots, and rhizomes were present in more stomachs ($F = 13.48$; $df = 1, 3$; $P = 0.03$) and with a greater relative abundance ($F = 9.79$; $df = 1, 3$; $P = 0.05$) during summer (49.4% occurrence, 20.3% abundance) than winter (18.9% occurrence, 8.6% abundance) (Table 3). I found this material in a greater proportion of stomachs ($F = 9.79$; $df = 1, 3$; $P = 0.05$) and with a greater relative abundance ($F = 9.81$; $df = 1, 3$; $P = 0.05$) in black rats (46.4% occurrence, 21.5% abundance) than in Polynesian rats (22.0% occurrence, 7.4% abundance). The percentage occurrence ($F = 0.39$; $df = 1, 3$; $P = 0.57$) and relative abundance ($F = 0.29$; $df = 1, 3$; $P = 0.63$) of this plant material in the diet of rats

was similar between HNAR (30.6% occurrence, 12.5% abundance) and WNP (36.6% occurrence, 15.7% abundance).

I did not find any bones or eggshells in any stomachs. One stomach each from HNAR and WNP contained small fragments of feathers that may have been consumed incidentally during foraging. Rodent fur and flesh were found only in stomachs of black rats and probably reflect cannibalism by this species on rats and mice that were found partially eaten in the snap traps. One to 3% of stomachs (1–2% relative abundance) from HNAR and 5–23% of stomachs (1–10% relative abundance) from WNP contained rodent remains (Table 3). The incidence of predation on trap-killed rats and mice was also higher at WNP (18 of 245 rat carcasses, 9 of 61 mice carcasses) than at HNAR (3 of 192 rat carcasses, 5 of 71 mice carcasses).

DISCUSSION

Published information on the abundance and biology of rodents in native Hawaiian forests is limited. This study indicates that black rats, Polynesian rats, and mice are abundant in HNAR and WNP during both winter and summer. The lack of Norway rats corroborates that this species is rare in high-elevation Hawaiian forests (Tomich 1986). Other investigators have found black and Polynesian rats to be abundant in low- and mid-elevation forests on the island of O'ahu (Tamarin and Malecha 1972), in Kīlauea forest (Tomich 1981) and Hakalau Forest National Wildlife Refuge (G. Lindsey, National Biological Service, pers. comm.) on the island of Hawai'i, and in Kīpahulu Valley on the southeastern slopes of Haleakalā, Maui (C. Stone, National Park Service, pers. comm.). My findings suggest that both black and Polynesian rats and mice are well adapted to the ecological conditions in rain forests on Maui.

Mice captures were high in HNAR and WNP during both winter and summer. In Hawai'i house mice usually are associated with drier grasslands, scrublands, and parklands (Tomich 1986). My findings and those of other investigators (C. Stone, L. Loope, National Park Service, pers. comm.) indicate that substantial mouse populations exist throughout the year in high-

elevation rain forests on Maui, especially above 1600 m. In the alpine shrubland of Haleakala National Park, Maui, the diet of mice consisted mainly of arthropods, fruits, and grasses (L. Loope, National Park Service, pers. comm.). Predation by mice on small eggs and nestlings of songbirds has been reported in New Zealand, although they are not considered important avian predators (Kikkawa 1966, Moors 1978). The impact of mice in native Hawaiian forest ecosystems is unknown. However, mice may be more important, especially during population irruptions, as competitors for food along with rats and as prey for mongooses, feral cats, and raptors than as avian predators.

I set traps only on the ground and thus may have missed rats that are active mainly in trees and rarely come to the ground. However, previous studies (Stone 1985, Tomich 1981) have indicated that black rats in Hawaiian forests are easily trapped both on the ground and in trees. Although Polynesian rats nest and feed in trees in New Zealand (Daniel 1969, Williams 1973) and on other Pacific islands (McCartney 1970, Fiedler et al. 1982), in Hawai'i they are only occasionally captured in the forest canopy (Stone 1985; G. Lindsey, National Biological Service, pers. comm.). Mice also are agile climbers and occasionally forage in trees (Dewbury et al. 1980, King 1990), but they spend most of their time on the ground (Tomich 1986).

I detected pregnancies in both Polynesian and black rats only in summer. Other investigators (Tomich 1981, Tamarin and Malecha 1972) have documented major breeding peaks from late spring to early autumn for black and Polynesian rats in similar habitats in other areas of Hawai'i. However, I recorded only late-term pregnancies that were obvious when I extracted the stomachs. This bias, together with small samples, precludes inferences about seasonal breeding patterns.

Invertebrates, particularly insect larvae, were the most frequently found and most abundant item in the stomachs of both black and Polynesian rats. Arthropods also predominated in the diets of black rats captured in wet montane forests of the Galápagos Islands (Clark 1982), Ponapei and adjacent islands (Strecker and Jackson 1962), and Malaya (Harrison 1957). The greater quantity of invertebrates in the diet of both black and Polynesian rats in winter than in

summer in Hawai'i may reflect an increased demand for protein or a relative scarcity of fleshy fruit and other preferred plant material during that period. Rats are opportunistic omnivores that vary their diets in relation to seasonal abundance of preferred foods in their habitat (Best 1969, Daniel 1973, Clark 1982, Bunn and Craig 1989). That young rats ate more invertebrates than did adults may indicate a requirement of growing animals for protein (Clark 1982).

Black rats in HNAR and WNP ate more fruits, seeds, and other plant matter than did Polynesian rats. Other investigations (Kami 1966, Norman 1970, Fall et al. 1971, Mosby and Wodzicki 1973, Clark 1982) also found Polynesian rats to have a more restricted diet than black rats. That both black and Polynesian rats included fruits, seeds, and other plant material in their diets during both trapping periods indicates that plant material, especially fruits and seeds, may be nutritionally important supplements, some of which are relatively scarce during winter (e.g., *Rubus* spp.).

Other than a couple of feather fragments, I did not find bird remains or bird eggs in any stomachs. Similar negative or incidental evidences of bird consumption by forest-trapped rats have been reported in Hawai'i (Russell 1980, Stone 1985, Amarasekare 1993) and New Zealand (Best 1969, Moors 1978). This, however, does not preclude the possibility that rats eat birds and eggs. Examination of rodent stomach contents is not a reliable indicator of the potential threat of rat predation to birds. Rats are fastidious feeders that may consume egg contents without actually ingesting eggshells. Also, rats can have a substantial impact on small prey populations even if they attack nestlings only sporadically.

Additional circumstantial evidence implicating rodents as avian predators in Hawaiian forests has been based on failed nests. Descriptions of shattered eggs or partly eaten chicks, disarranged and destroyed nests, and mysterious nest abandonment have been reported for selected endangered Hawaiian forest birds (Van Riper 1978, Pletschet and Kelly 1990, Amarasekare 1993; P. Banko, National Biological Service, pers. comm.). Laboratory feeding trials in New Zealand (Moors 1978) established that such signs at plundered nests were characteristic of

nests visited by black rats and mice. Factors such as avian life cycle, nest accessibility, and nest odors or nestling behavior that may attract rodents to nests need to be examined and may provide clues on the vulnerability of adult birds, chicks, and eggs to predation. The bird breeding season on Maui extends from January to May, and rodents may prey upon them opportunistically, such as when eggs and nestlings are present and most vulnerable to predation. Even if avian prey forms only a small proportion of a rodents's diet and the number of depredated nests are few, even the smallest losses to predation can be sufficient to decrease breeding success and tip the balance against endangered Hawaiian forest birds.

Besides direct effects of bird predation, rodents may compete with Hawaiian forest birds for food and nesting sites. My results show that Polynesian and black rats consume a variety of invertebrate and plant foods. During periods when these resources are scarce, rats and mice may compete with native birds that rely on these food resources. Scott et al. (1986) suggested that rodents may limit the distribution and numbers of frugivorous and nectivorous birds by competing with them for preferred fruits, seeds, or nectar resources. Rodents may also compete with insectivorous birds that have restricted diets or substrate foraging capabilities (Banko and Banko 1976), such as birds that forage on branches and trunks for burrowing larvae, pupae, and adult insects (Baldwin and Casey 1983, Scott et al. 1986). Radio-telemetry studies have shown that black rats in the Hakalau Forest National Wildlife Refuge on the island of Hawai'i utilize 'ōhi'a and koa trunk cavities for denning and nesting (G. Lindsey, National Biological Service, pers. comm.). The 'Ākepa (*Loxops coccineus*), an endangered Hawaiian honeycreeper, is also known to use similar cavity nests. However direct evidence of rodents competing with native Hawaiian forest birds for preferred habitat and food resources is lacking. Further studies are needed to determine if rodents and native birds overlap in their use of these resources.

Native species of flightless crickets and earwigs are rare on all Hawaiian islands except Nihoa, where rats are rare or absent (Conant et al. 1984). As much as 50% of Hawai'i's endemic

land snails and a large number of arthropods have already been lost (Howarth et al. 1988), and some of the remaining species are susceptible to predation by rats (Gagné and Christensen 1985). Two genera of native tree snails, *Achatinella* on O'ahu and *Partulina* on Maui, occur only in small, isolated forest populations (Gagné and Christensen 1985, Hadfield et al. 1993) where rats are common and may be limiting the number of these endangered mollusks.

Conservation of Hawai'i's native forest ecosystem clearly requires reducing or controlling the impacts of introduced plants and animals, including rodents. HNAR and WNP are two of the few remaining habitats of rare native Hawaiian forest birds, plants, and invertebrates, whose numbers and range have been drastically declining in recent years. Introduced rodents undoubtedly can have a serious impact on the forest ecosystem and have a contributing role in this decline. The serious and immediate nature of this threat, together with the common concerns of biologists, conservationists, and land managers in Hawai'i have recently resulted in regulatory approval for use of an anticoagulant rodenticide bait in native wilderness areas in Hawai'i to mitigate rat depredations. Further studies are needed to better understand the life history, ecology, and behavior of these predators, document their impacts on the native ecosystem in other areas, and evaluate available techniques (e.g., trapping, rodenticide baits) in large-scale operational control programs. Only then can sound recommendations be made in formulating biologically and economically practical rodent control strategies to protect Hawai'i's unique plant and animal resources.

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LITERATURE CITED

- AMARASEKARE, P. 1993. Potential impact of mammalian nest predators on endemic forest birds of western Mauna Kea, Hawaii. *Conserv. Biol.* 7:316-324.
- ATKINSON, I. A. E. 1977. A reassessment of factors, particularly *Rattus rattus* L., that influenced the decline of endemic forest birds in the Hawaiian islands. *Pac. Sci.* 31: 109-133.
- . 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. Pages 35-81 in P. J. Moors, ed. *Conservation of island birds*. International Council for Bird Preservation Tech. Publ. 3. Cambridge, England.
- . 1989. Introduced animals and extinctions. Pages 54-79 in D. Western and M. C. Pearl, eds. *Conservation for the twenty-first century*. Oxford University Press, New York.
- BAKER, J. K., and S. ALLEN. 1976. Studies on the endemic Hawaiian genus *Hibiscadelphus* (*ha-kuahiwi*). Pages 19-22 in C. W. Smith, ed. *Proceedings, Hawaii Volcanoes National Park 1st Natural Science Conference, Cooperative National Park Resources Studies Unit*. University of Hawai'i, Honolulu.
- BALDWIN, P. H., and T. L. C. CASEY. 1983. A preliminary list of foods of the Po'o-uli. *Elepaio* 43:53-56.
- BANKO, W. E., and P. C. BANKO. 1976. Role of food depletion by foreign organisms in historical decline of Hawaiian forest birds. Pages 29-34 in C. W. Smith, ed. *Proceedings, Hawaii Volcanoes National Park 1st Natural Science Conference, Cooperative National Park Resources Studies Unit*. University of Hawai'i, Honolulu.
- BERGER, A. J. 1981. *Hawaiian birdlife*, 2nd ed. University of Hawai'i Press, Honolulu.
- BEST, L. W. 1969. Food of the roof rat (*Rattus rattus rattus* L.) in two forest areas of New Zealand. *N. Z. J. Sci.* 12:258-267.
- BUCKLE, A. P., and M. G. P. FENN. 1992. Rodent control in the conservation of endangered species. Pages 36-41 in J. E. Borrecco and R. E. Marsh, eds. *Proceedings, 15th Conference, Vertebrate Pest Council*. University of California, Davis.
- BUNN, T. J., and J. L. CRAIG. 1989. Population cycles of *Rattus exulans*: Population changes, diet, and food availability. *N. Z. J. Zool.* 16:409-418.

- BUXBAUM, K. 1973. Status of the dark-rumped petrel on Maui, 1972. *Elepaio* 34:11–12.
- CLARK, D. A. 1982. Foraging behavior of a vertebrate omnivore (*Rattus rattus*): Meal structure, sampling, and diet breadth. *Ecology* 63:763–772.
- CONANT, S., C. C. CHRISTENSEN, P. CONANT, W. C. GAGNÉ, and M. L. GOFF. 1984. The unique terrestrial biota of the Northwestern Hawaiian Islands. Pages 77–94 in R. W. Grigg and K. Y. Tanoue, eds. *Proceedings of the 2nd Symposium on Resource Investigations in the Northwestern Hawaiian Islands* 1:77–94.
- DANIEL, M. J. 1969. A survey of rats on Kapiti Island, New Zealand. *N. Z. J. Sci.* 12:363–372.
- . 1973. Seasonal diet of the ship rat (*Rattus rattus*) in lowland forest in New Zealand. *Proc. N. Z. Ecol. Soc.* 20:21–30.
- DEWBURY, D. A., D. L. LANIER, and A. MIGLIETTA. 1980. A laboratory study of climbing behavior in 11 species of muroid rodents. *Am. Midl. Nat.* 103:66–72.
- FALL, M. W., A. B. MEDINA, and W. B. JACKSON. 1971. Feeding patterns of *Rattus rattus* and *Rattus exulans* on Eniwetok Atoll, Marshall Islands. *J. Mammal.* 52:69–76.
- FIEDLER, L. A., M. W. FALL, and R. F. REIDINGER, JR. 1982. Development and evaluation of methods to reduce rat damage to coconut in the Philippines. Pages 73–79 in R. E. Marsh, ed. *Proceedings, 10th Conference, Vertebrate Pest Council, University of California, Davis*.
- FLEET, R. R. 1972. Nesting success of the red-tailed tropicbird on Kure Atoll. *Auk* 89:651–659.
- GAGNÉ, W. C., and C. C. CHRISTENSEN. 1985. Conservation status of native terrestrial invertebrates in Hawaii. Pages 105–126 in C. P. Stone and J. M. Scott, eds. *Hawai'i's terrestrial ecosystems: Preservation and management*. Cooperative National Park Resources Studies Unit. University of Hawai'i, Honolulu.
- HADFIELD, M. G., S. E. MILLER, and A. H. CARWILE. 1993. The decimation of endemic Hawaiian tree snails by alien predators. *Am. Zool.* 33:610–622.
- HARRISON, J. L. 1957. Habitat of some Malayan rats. *Proc. Zool. Soc. Lond.* 128:1–21.
- HOWARTH, F. G., S. H. SOHMER, and W. D. DUCKWORTH. 1988. Hawaiian natural history and conservation efforts. *BioScience* 38:232–237.
- HYNES, H. B. N. 1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *J. Anim. Ecol.* 19:36–58.
- KAMI, H. T. 1966. Foods of rodents in the Hamakua District, Hawaii. *Pac. Sci.* 20:367–373.
- KEPLER, C. B. 1967. Polynesian rat predation on nesting Laysan albatrosses and other Pacific seabirds. *Auk* 84:426–430.
- KIKKAWA, J. 1966. Population distribution of land birds in temperate rain forest of southern New Zealand. *Trans. R. Soc. N. Z. Zool.* 7:215–277.
- KING, C. M., ed. 1990. *The handbook of New Zealand mammals*. Oxford University Press, Auckland.
- KIRCH, P. 1982. The impact of the prehistoric Polynesians on the Hawaiian ecosystem. *Pac. Sci.* 36:1–14.
- MCCARTNEY, W. C. 1970. Arboreal behavior of the Polynesian rat (*Rattus exulans*). *BioScience* 20:1061–1062.
- MOORS, P. J. 1978. Methods for studying predators and their effects on forest birds. Pages 47–57 in P. R. Dingwall, I. A. E. Atkinson, and C. Hay, eds. *The ecology and control of rodents in New Zealand nature reserves*. N. Z. Dep. Lands Surv. Info. Ser. 4. Wellington.
- MOORS, P. J., I. A. E. ATKINSON, and G. H. SHERLEY. 1992. Reducing the rat threat to island birds. *Bird Conserv. Int.* 2:93–114.
- MOSBY, J. M., and K. WODZICKI. 1973. Food of the Kimoa (*Rattus exulans*) in the Tokelau Islands and other habitats in the Pacific. *N. Z. J. Sci.* 16:799–810.
- NORMAN, F. I. 1970. Food preferences of an insular population of *Rattus rattus*. *J. Zool.* 162:493–503.
- PLETSCHET, S. M., and J. F. KELLY. 1990. Breeding biology and nesting success of Palila. *Condor* 92:1012–1021.
- RUSSELL, C. A. 1980. Food habits of the roof rat (*Rattus rattus*) in two areas of Hawaii Volcanoes National Park. Pages 269–272 in

- Proceedings, 3rd Hawaii Volcanoes National Park Natural Science Conference, Cooperative National Park Resources Studies Unit, University of Hawai'i, Honolulu.
- SAS INSTITUTE. 1988. SAS/STAT user's guide, version 6.03. SAS Institute, Cary, North Carolina.
- SAVILLE, D. J. 1990. Multiple comparison procedures: The practical solution. *Am. Stat.* 44:174-180.
- SCOTT, J. M., S. MOUNTAINSPRING, F. L. RAMSEY, and C. B. KEPLER. 1986. Forest bird communities of the Hawaiian Islands: Their dynamics, ecology, and conservation. *Stud. Avian Biol.* 9.
- SCOWCROFT, P. G., and H. F. SAKAI. 1984. Stripping of *Acacia koa* bark by rats on Hawaii and Maui. *Pac. Sci.* 38:80-86.
- SIMONS, T. R. 1983. Biology and conservation of the endangered Hawaiian Dark-rumped Petrel (*Pterodroma phaeopygia sandwichensis*). Cooperative National Park Resources Studies Unit Tech. Rep. 83-2. University of Washington, Seattle.
- STONE, C. P. 1985. Alien animals in Hawai'i's native ecosystem: Toward controlling the adverse effects of introduced vertebrates. Pages 251-297 in C. P. Stone and J. M. Scott, eds. *Hawai'i's terrestrial ecosystems: Preservation and management*. Cooperative National Park Resources Studies Unit. University of Hawai'i, Honolulu.
- STRECKER, R. L., and W. B. JACKSON. 1962. Habitats and habits. Pages 64-73 in T. I. Storer, ed. *Pacific island rat ecology*. Bernice P. Bishop Mus. Bull. 225.
- TAMARIN, R. H., and S. R. MALECHA. 1972. Reproductive parameters in *Rattus rattus* and *Rattus exulans* of Hawaii, 1968 to 1970. *J. Mammal.* 53:513-528.
- TOBIN, M. E., and R. T. SUGIHARA. 1992. Abundance and habitat relationships of rats in Hawaiian sugarcane fields. *J. Wildl. Manage.* 56:816-822.
- TOMICH, P. Q. 1981. Community structure of introduced rodents and carnivores. Pages 301-309 in D. Mueller-Dombois, K. W. Bridges, and H. L. Carson, eds. *Island ecosystems, US/Int. Biol. Prog. Synthesis Ser. 15*. University of Hawai'i Press, Honolulu.
- . 1986. *Mammals in Hawai'i*, 2nd ed. Bishop Museum Press, Honolulu.
- VAN RIPER, C., III. 1978. The breeding biology of the Amakihi (*Loxops virens*) and Palila (*Psittirostra bailleui*) on Mauna Kea, Hawaii. Ph.D. diss., University of Hawai'i, Honolulu.
- WILLIAMS, J. M. 1973. The ecology of *Rattus exulans* (Peale) revisited. *Pac. Sci.* 27: 120-127.