

**The Hawai'i-Pacific Islands Cooperative Ecosystems Studies Unit &  
Pacific Cooperative Studies Unit  
UNIVERSITY OF HAWAII AT MĀNOA**

Dr. David C. Duffy, Unit Leader  
Department of Botany  
3190 Maile Way, St. John #408  
Honolulu, Hawai'i 96822



Technical Report 183

**Population dynamics of introduced rodents in Hawai'i Volcanoes  
National Park 1986-1990**

April 2012

Pamela Y. Scheffler<sup>1,2</sup>, David Foote<sup>3</sup>, Charlotte Forbes Perry<sup>1,2</sup>, Karin Schlappa<sup>1,2</sup>, and  
Charles P. Stone<sup>4</sup>

<sup>1</sup> Pacific Cooperative Studies Unit, University of Hawai'i at Mānoa, Department of Botany, 3190 Maile Way Honolulu, Hawai'i 96822.

<sup>2</sup> NPS Inventory and Monitoring Program, Pacific Island Network, PO Box 52, Hawai'i National Park, HI 96718.

<sup>3</sup> U.S. Geological Survey, Pacific Island Ecosystems Research Center, Kīlauea Field Station, P.O. Box 44, Hawai'i National Park, HI 96718.

<sup>4</sup> Eagles Nest Lakes, Ely, MN 55731.

**PCSU is a cooperative program between the University of Hawai'i and U.S. National Park Service, Cooperative Ecological Studies Unit.**

**Organization Contact Information:**

U.S. Geological Survey, Pacific Island Ecosystems Research Center, Kīlauea Field Station, P.O. Box 44, Hawai'i National Park, HI 96718.

**Recommended Citation:**

Scheffler, P.Y., D. Foote, C.F. Perry, K. Schlappa, and C.P. Stone. 2012. Population dynamics of introduced rodents in Hawai'i Volcanoes National Park 1986-1990. Technical Report No. 183. Pacific Cooperative Studies Unit, University of Hawai'i, Honolulu, Hawai'i. 48 pp.

**Key words:**

Invasive rodents, black rats, *Rattus*, *Mus*, population dynamics

**Place key words:**

Kamoamoa, Kipuka Puauulu, Mauna Loa, Naulu, Olaa Forest, Hawaii Volcanoes National Park, Hawaii

Editor: David C. Duffy, PCSU Unit Leader (Email: [dduffy@hawaii.edu](mailto:dduffy@hawaii.edu))

Series Editor: Clifford W. Morden, PCSU Deputy Director (Email: [cmorden@hawaii.edu](mailto:cmorden@hawaii.edu))

**About this technical report series:**

This technical report series began in 1973 with the formation of the Cooperative National Park Resources Studies Unit at the University of Hawai'i at Mānoa. In 2000, it continued under the Pacific Cooperative Studies Unit (PCSU). The series currently is supported by the PCSU and the Hawai'i-Pacific Islands Cooperative Ecosystem Studies Unit (HPI CESU).

The Pacific Cooperative Studies Unit at the University of Hawai'i at Mānoa works to protect cultural and natural biodiversity in the Pacific while encouraging a sustainable economy. PCSU works cooperatively with private, state and federal land management organizations, allowing them to pool and coordinate their efforts to address problems across the landscape.

The Hawai'i-Pacific Islands Cooperative Ecosystem Studies Unit is a coalition of governmental agencies, non-governmental organizations and universities that promotes research, education and technical assistance to support better stewardship of imperiled natural and cultural resources within the Pacific.

The HPI CESU is one of 17 cooperative ecosystem studies units across the U.S.

## TABLE OF CONTENTS

List of Tables.....	iv
List of Figures.....	iv
Abstract.....	1
Introduction.....	1
Study Sites.....	3
Methods.....	4
Field Methods.....	4
Laboratory Analysis.....	4
Data Analysis.....	4
Results.....	6
Capture Rate.....	7
Age Structure.....	8
Female Reproduction.....	10
Sex Ratio.....	11
Size.....	12
Movement Patterns.....	13
Pelage Color.....	13
Discussion.....	14
Conclusions.....	18
Acknowledgments.....	19
Literature Cited.....	20

## LIST OF TABLES

Table 1. Trapping schedule for rodents at five sites in Hawai'i Volcanoes National Park, Hawai'i.....	24
Table 2. The mean number of captures per trap night per trapping session by species at five study sites in Hawai'i Volcanoes National Park, Hawai'i.....	24
Table 3. The median weight at sexual maturity for rodent species captured at each of five sites in Hawai'i Volcanoes National Park, Hawai'i .....	25
Table 4. Distances traveled by rodent species at the 'Ōla'a Small Tract and Lowlands of Hawai'i Volcanoes National Park, Hawai'i.....	25

## LIST OF FIGURES

Figure 1. The location of the five study areas within Hawai'i Volcanoes National Park, Hawai'i.....	26
Figure 2. The location of the Kamoamoā transect in the Lowlands.....	27
Figure 3. The location of the two Nāulu transects in the Lowlands .....	28
Figure 4. The location of the transects in the 'Ōla'a Large and 'Ōla'a Small Tract .....	29
Figure 5. The location of the two transects at Kīpuka Puāulu .....	30
Figure 6. The location of the four transects at the Mauna Loa Strip site .....	31
Figure 7. Rodent species composition from the five study sites.....	32
Figure 8. Capture rate for rodents trapped at the Mauna Loa Strip.....	33
Figure 9. The mean number of rodents caught at the five study sites.....	34
Figure 10. Capture rate for rodents trapped at Kīpuka Puāulu.....	35
Figure 11. Capture rate for rodents trapped at 'Ōla'a Large Tract.....	36
Figure 12. Capture rate for rodents trapped at 'Ōla'a Small Tract.....	37
Figure 13. Capture rate for rodents in the Lowlands .....	38
Figure 14. Age structure for rodent captures at the Mauna Loa Strip.....	39
Figure 15. Age structure for rodent captures at Kīpuka Puāulu.....	40
Figure 16. Age structure for rodent captures at the 'Ōla'a Large Tract.....	41
Figure 17. Age structure for rodent captures at the 'Ōla'a Small Tract.....	42
Figure 18. Age structure for rodent captures in the Lowlands.....	43
Figure 19. The mean percentage of reproductive female rodents across seasons at the five study sites.....	44
Figure 20. Seasonal sex ratio for the four rodent species at the five study sites.....	45
Figure 21. Mean weight of the four rodent species found at the five study sites in Hawai'i Volcanoes National Park .....	46
Figure 22. Distances traveled by the three most common species of rodents in the 'Ōla'a Small Tract.....	47
Figure 23. Seasonal change in pelage color for black rats at the five study sites .....	48

## ABSTRACT

We determined seasonal and geographical distribution patterns for four species of introduced rodents in Hawai'i Volcanoes National Park from 1986-1990. We surveyed black rats (*Rattus rattus*), Polynesian rats (*R. exulans*), Norway rats (*R. norvegicus*) and house mice (*Mus musculus*) along an elevation gradient ranging from 90–1,820 m above sea level in five different sites using baited snap traps. Rodent community structure differed by elevation: there were more mice at montane sites and more Polynesian rats in the lowlands. We found that breeding occurred throughout the year for all species at all sites but that seasonal peaks in reproductive activity were common. Reproduction tended to be more common in the summer months at higher elevation sites and in the winter months at lower elevations. Rodents of all species were more abundant in our study in the winter than in the summer, but the differences were not significant. The overall sex ratio did not vary from a 1:1 ratio, but seasonally there were differences in sex ratio which varied with species and site. We calculated the minimum distance traveled from an assessment line and found that larger-bodied species traveled longer average distances. Pelage color in black rats was darkest in wet forest which may have adaptive value. Black and Polynesian rats were widespread in almost all habitat types, whereas mice were limited to dry and mesic sites; Norway rats were the rarest component of our sampling and found only in wet montane forest ('Ōla'a Forest).

## INTRODUCTION

Introduced rodents alter ecosystems throughout the world (Fukami et al. 2006; Simberloff, 2009). They have impacted native communities in the northern (Major and Jones 2005) and southern (Harper et al. 2005) hemispheres and from the Atlantic (Ganzhorn 2003, Abdelkrim et al. 2004, Delgado García et al. 2005, Nogales et al. 2006) to the Pacific (Atkinson 1977, Clark 1981, Harper et al. 2005, Jones et al. 2006). Rodent invasions on oceanic islands, such as Hawai'i, have been especially damaging to endemic biota (Mooney and Hobbs 2000, Towns et al. 2006, Athens 2009).

Prior to human settlement, the Hawaiian Islands had no terrestrial mammals except the endemic Hawaiian hoary bat (*Lasiurus cinereus semotus*) (Tomich 1986). Polynesian rats (*Rattus exulans*) were introduced with some of the first human populations that voyaged to the islands and have been present in lowland habitats since about AD 1000 (Athens, 2009). Other rodents arrived with subsequent European explorers: the house mouse (*Mus musculus*) was established by 1816 (Kotzebue 1821 in Atkinson 1977), the Norway rat (*R. norvegicus*) by 1835 (Atkinson 1977), and the black or roof rat (*R. rattus*) by the late 1800s (Atkinson 1977). Today these four species are found on most major islands in the Pacific Ocean, in many different vegetation types and across a wide range of elevations. Although the Polynesian rat reportedly favors the lowlands and the black rat prefers low to mid-elevations (Tomich 1981), both species are wide-ranging and found at higher elevations, sometimes in substantial numbers (C. P. Stone, unpublished data). For example, the black rat is found as high as 2,440 m in Hawai'i Volcanoes National Park (Tomich 1981) and both black and Polynesian rats have been found as high as 2,950 m in Haleakalā National Park (Tomich 1969, Tobin 1994). Norway rats are also most commonly found at lower elevations, but, in part due to their association with humans, are capable of establishing at upper elevations as well (Timm 1994b).

Rodents cause many economic, health and ecological problems throughout the Hawaiian Islands (Tomich 1986). As major crop pests, rats have been very damaging to the sugar cane industry (Atkinson 1977). Damage by black rats to the macadamia nut industry is estimated at \$2–4 million annually (Marsh 1994). Nationwide, they are believed to cause several billion dollars in crop damage (Pimentel et al. 2005).

Rats are known vectors of human disease and have a long history as carriers of the plague (*Yersinia pestis*) (Tomich 1986). In Hawai‘i, black rats carry leptospirosis, a disease characterized by high fever which often leads to meningitis. They also act as a reservoir for the nematode parasite *Angiostrongylus cantonensis*, the causative agent of angiostrongylosis. This is a potentially fatal disease vectored by slugs (including helicarionids and veronicellids) that can also lead to meningitis and pulmonary or gastrointestinal illness in humans (Hollingsworth et al. 2007).

Rodents consume seeds of native plants (Male and Loeffler 1997, Sugihara 1997), decreasing or preventing regeneration (Allen 2000, Cabin et al. 2000). Food selection is seasonal. Although black rats primarily eat plant material in relation to its abundance in the environment (Russell 1980), both black rats and mice are selective in their choice of plant material, preferring high-energy plant material in excess to its abundance (Cole et al. 2000). Damage to plants can be quite severe. For example, during one population irruption, black rats were observed to have destroyed nearly every ‘ie‘ie (*Freycinetia arborea*) fruit in O‘ahu forests (Perkins 1903 in Atkinson 1977), thereby preventing regeneration and depriving the (now almost certainly extinct) o‘u (*Psittirostra psittacea*) bird of one of its main food sources. In addition to acting as seed predators, it has also been recently demonstrated that black rats can act as seed dispersers, especially for fruits consumed bearing small seeds (Shiels 2011, Shiels and Drake 2011).

Rodents are known to consume native invertebrates. On Maui, native arthropods comprised a large percentage of the stomach content of black rats, Polynesian rats, and mice (Sugihara 1997, Cole et al. 2000). The proportion of native arthropods in rodent diets was substantially larger in months when plant material was scarce (Cole et al. 2000). It appears that mice have a large impact on native arthropod populations; their diet is especially high in native Lepidoptera larvae in both Hawai‘i (Cole et al. 2000) and New Zealand (Ruscoe 2001). Other types of endemic Hawaiian invertebrates also have been affected by the introduction of rats. Many species of native Hawaiian land snails, once very numerous, are now extinct largely due to black rat predation (Baldwin 1887 in Atkinson 1977, Myers and Shiels 2009).

Native Hawaiian species evolved in the absence of mammalian predators and have little defense against rodents. Rodents (especially black rats) have been implicated in the decline of native passerine birds (Atkinson 1977) and local extirpation of the Laysan Finch (*Telespyza cantans*) and the extinction of the Laysan rail (*Porzanula palmeri*) and Hawaiian rail (*Porzana sandwichensis*) (Tomich 1969, Berger 1981, Gorresen et al. 2009). Black rats are very good climbers and often prey on eggs, nestlings, and sitting adults. Predation by black rats is one of the largest causes of nest failure for many species of native Hawaiian birds (Amarasekare 1993, Levy 2003). Removal of black rats from bird habitat has been shown to increase chick survival of Wedge-tailed Shearwaters (*Puffinus pacificus*) in Hawaii (Smith et al. 2006). Black rats have

been implicated in the decline and extinction of the native avifauna on other Pacific Islands (such as New Zealand) (Diamond and Veitch 1981, Towns et al. 2006).

Despite the documented impacts of rodents in island ecosystems, there is a paucity of information concerning the distribution and relative abundance of the different species in native communities. The objective of this study was to determine population characteristics of introduced rodents across a range of vegetation types in Hawai'i Volcanoes National Park. This important historical survey of rodents from the late 1980s can serve as a baseline to evaluate long-term changes in the distribution and abundance of invasive rodents in the park.

## STUDY SITES

The study was conducted during 1986-1990 in Hawai'i Volcanoes National Park (HAVO), on both Kīlauea and Mauna Loa Volcanoes of Hawai'i Island. Five sites spanning different elevation zones and native vegetation types were selected for sampling (Figure 1). Two sites were sampled in the coastal lowlands of the Park. The Kamoamoā site was approximately 1.4 km north of the Kamoamoā campground in a 52-ha kīpuka at 90-180 m elevation (Figure 2). The substrate was 'a'ā aged 500-750 years from Kīlauea's East Rift (Holcomb 1987), and vegetation was predominantly lama/'ōhi'a (*Diospyros sandwicensis*/*Metrosideros polymorpha*) mesic forest (Stemmerman and Ihle 1993). After the study, this site was covered by lava from the ongoing Kīlauea eruption. The second lowland site was Nāulu Forest, two kīpuka with remnant lama/'ōhi'a dry to mesic forest located on the south-facing slope of Hōlei Pali between 400 and 600 m elevation (Figure 3). Transects were established in the easternmost kīpuka of Nāulu forest and in a second kīpuka positioned below the Kealakomo shelter. These two kīpuka ranged in size from 41 to 49 ha and were separated by the 1972 Mauna Ulu lava flow. Both kīpuka had substrates of 'a'ā, with ages estimated at 500-750 years before present (Holcomb 1987).

Two transects were established in montane wet forest in 'Ōla'a Forest, a disjunct section of 'ōhi'a/hāpu'u (*M. polymorpha*/*Cibotium* spp.) rainforest that is located approximately 2 km east of the main park boundary (Figure 4). Transects were placed in small tract of 'Ōla'a Forest (144 ha) and the large tract (3,765 ha), adjacent to Wright Road at approximately 1,160 m elevation; known collectively as Ola'a Tract, both tracts are on deep ash soil over Mauna Loa substrate greater than 4,000 years old (Lockwood et al. 1988). The small tract was surrounded by pasture and residential lots on three sides and flanked by Wright Road on the fourth side. The large tract was bounded by farm lots, the Pu'u Maka'ala Natural Area Reserve, and pasture. At the time of the study, feral pigs (*Sus scrofa*) had been eradicated from 'Ōla'a Forest in the small tract but were still common in the large tract. A complete site description is found in Pratt and Abbott (1997).

A montane mesic site was selected at Kīpuka Puaulu, a 42 ha mixed koa/'ōhia/soapberry (*Acacia koa*, *M. polymorpha*, *Sapindus saponaria*) forest on deep ash soil at 1,200 m elevation (Figure 5). This kīpuka supports one of the most diverse and species-rich plant communities in the Park (Mueller-Dombois and Lamoureux 1967)..

The highest elevation site was established in montane dry koa forest at Kīpuka Kulalio on Mauna Loa between 1,615 and 1,800 m elevation (Figure 6). Transects were placed at three forested

sites near the Mauna Loa Strip Road (currently shown on maps as Mauna Loa Road). The substrate of this area is weathered pāhoehoe with shallow ash deposits; one additional transect was adjacent to an arm of the late prehistoric Ke‘āmoku Lava Flow.

## METHODS

### Field Methods

Four 500 m transects were established in the Mauna Loa site, one at Kamoamoā, and two each at Kīpuka Puāulu, Nāulu, and two at the ‘Ōla‘a Forest tracts (Figures 1–6). Transects were pre-baited with grated coconut four days prior to trapping. One hundred (100) Victor brand snap-type rat traps were placed at 5-m intervals along these transects and baited with a 2 cm<sup>3</sup> piece of coconut. Trapping was conducted for a period of eight consecutive nights: traps were checked by 10:00 am each morning; trapped animals were tagged and removed to reduce scavenging by mongoose (*Herpestes auropunctatus*) and other rats. Traps were reset and missing bait was replaced at the time that animals were removed. Each of the five areas was sampled four times during the period from 1986–1990 and Kīpuka Puāulu was sampled five times during this period (Table 1). Traps were removed between trapping periods.

To determine movement patterns, a 780 m assessment line transect was established for each transect or group of transects. At ‘Ōla‘a Forest, an assessment line was established in both the large and small tracts. The lines were placed at a 54° angle to the transects, crossing at 390 m on the OS-2 and OL-2 transects; the assessment lines did not intersect the OS-4 and OL-4 transects. At Kamoamoā, the assessment line and trapping transect began at the same location; the assessment line was established at a 39° angle to the trapping transect. At Nāulu and Mauna Loa, assessment lines were established at the terminal end of each of the transects at a 39° angle to the transects. On the first and third day of trapping, shredded coconut mixed with a pink fluorescent particulate was scattered along the assessment lines. Presence or absence of the particulate was determined in the laboratory by examining stomach contents under UV light. The location of the assessment line at Kīpuka Puāulu could not be determined from the historical data used to prepare this summary.

### Laboratory Analysis

Captured animals were brought back to the lab for analysis. Species identifications were made for all individuals unless identification was impossible (e.g., in the case of poorly preserved or cannibalized specimens). The sex, and sexual maturity (scrotal males and lactating or pregnant females were considered sexually mature), and the number of embryos, if pregnant, were recorded. We weighed individuals using a Pesola scale accurate to one gram, and measured the length of the body, tail, hind foot, and ear-to-notch to the nearest millimeter. Pelage color (black, agouti white, or agouti grey) was noted for black rats. Stomachs and jaws were collected and preserved for later analysis. However, we do not report on these methods here since results of this part of the study will be published in a separate manuscript.

### Data Analysis

Data were analyzed using SYSTAT 11.00.01 (Systat Software, Inc. 2004). Transformations were attempted for data with non-normal distributions and non-parametric statistics were used when transformations did not improve the normality of the distribution.



Trap success was measured as the number of captures of a given species per 100 trap nights (trap night = one open trap over a one night period), corrected for missing and sprung traps (Beauvais and Buskirk 1999). The mean number of rodents per 100 corrected trap nights was calculated for each trapping period, and trapping success was compared between habitats for each of the four rodent species. Black and Polynesian rat captures followed a normal distribution and were analyzed with parametric Analysis of Variance (ANOVA); Norway rats and mice were analyzed using Kruskal-Wallis tests. To determine if there was a difference in trapping success over the eight-day trapping period, the number of captures per trap night by day was compared using Kruskal-Wallis analysis for all species. Seasonality in abundance was determined by comparing the average number of daily captures across seasons using ANOVA and Kruskal-Wallis tests.

Chronological age is difficult to determine in rodents and weight is often used as an index of age (Davis 1953, Tamarin and Malecha 1971). We classified rodents as either adult or sub-adult based on sexual maturity and weight: all sexually mature individuals, as well as those weighing equal to or more than the median weight at maturity (as calculated by sex for each site, using the methodology described in Davis 1956), were classified as adults and the remainder were considered sub-adults. In addition, we used the median weight at sexual maturity for males and for females (Davis 1956) of each rodent species for between-site comparison of general vigor.

Reproductive females were classified as either lactating or pregnant. The proportion of actively reproductive females was calculated for each species by season and compared using one-way ANOVA or Kruskal-Wallis U tests. The mean number of embryos per female was calculated and compared across species and across seasons for each species, using ANOVA tests.

Sex ratio was determined for each of the rodent species trapped and compared to an expected 1:1 ratio using chi-square tests. We compared the sex ratio of all trapping periods combined, as well as those of the individual trapping periods. Trapping periods were divided into season (winter = December–February, spring = March–May, summer = June–August, fall = September–November) to determine seasonal differences in sex ratio. Trapping sessions that occurred over two months in different season classes were placed in the season during which more trap days were conducted (i.e., a trapping session that was conducted from February 23–March 02 was considered winter trapping).

Movement patterns were analyzed for individuals with fluorescent dye in their stomachs (indicating that the individual had been foraging along the assessment line). The minimum distance traveled from the assessment line to the trap station at which the individual was captured was calculated and minimum, maximum and average minimum distance traveled was calculated for each species at each site. Comparisons between species were made using Tukey's HSD at  $\alpha = 0.05$ .

Analysis for seasonal differences is based on the survey periods presented in Table 1. Given that seasonal differences in temperature are small in the tropics, particularly at lower elevation sites, the presented seasonal patterns should be looked at as differences between groups of months rather than as between true seasons.

## RESULTS

A total of 2,639 rodents were caught in 39,726.5 corrected trap nights. Black rats (*Rattus rattus*), Polynesian rats (*R. exulans*) and mice (*Mus musculus*) were present at all sites. Norway rats (*R. norvegicus*) were captured only at the 'Ōla'a sites. Other species captured in the snap traps included birds and mongooses but rodents were by far the most common taxon captured, ranging from 93-100% of the total capture at each site.

In the montane dry forest area, where we trapped for a total of 12,464.5 corrected trap nights, rodents comprised 93% of the identified capture (one specimen was lost before identification and another had been mostly eaten prior to collection from the trap). We also captured four species of alien birds and one native bird. Mice were the most common rodent species with 66% of the rodent capture (n = 542), followed by black rats at 33%, (n = 274); Polynesian rats were not common in this habitat, comprising only 1% (n = 12) of the rodent capture (Figure 7a).

At Kīpuka Puauulu (7,468 corrected trap nights), rodents comprised 94% of the identified capture (12 captures were unidentifiable). We also captured mongoose and at least five species of non-native birds. Black rats were the most common rodent species (43% of rodent captures, n = 351), followed by Polynesian rats (30%, n = 248) and mice (27%, n = 220; Figure 7b).

Rodents comprised 235 of 236 captures in the large tract at 'Ōla'a Forest in 6,046.5 corrected trap nights (the single non-target capture was a Northern Cardinal (*Cardinalis cardinalis*)). Of the four species of rodents captured, black rats were the most common (72% of the rodent capture, n = 169), followed by Norway (17%, n = 40), and Polynesian rats (10%, n = 23). Mice were uncommon in this habitat, comprising only 1% (n = 3) of the total rodent capture (Figure 7c). Because of the relative rarity of mice in this habitat, population parameters for this group are not discussed further.

There were a total of 458 captures over 6,038.5 corrected trap nights in the Small Tract of 'Ōla'a. Only 1% of these captures were species other than rodents (2 mongoose, 2 cardinals, and 1 unknown species). Of the rodent species captured, black rats were the most common (71% of the rodent capture, n = 285), followed by Polynesian (26%, n = 155), and Norway rats (2%, n = 11). Mice comprised less than 1% (n = 2) of the rodent capture (Figure 7d) and are not discussed further for this habitat.

In the Lowlands, where there were a total of 9,308.5 corrected trap nights (3,132 at Kamoamoā and 6,176.5 at Nāulu), Polynesian (43% of rodent capture, n = 221) and black rats (39%, n = 196) were the most common rodent species. Mice comprised 18% (n=92) of the total rodent capture (Figure 7e). At Nāulu, rodents comprised 99% (433 individuals) of the total capture and mongoose (6 individuals) comprised the remaining 1%. A single unidentified capture represented <1% of the total. At the two lowland sites, black rats made up 34% of the total rodents captured, Polynesian 45%, and mice 21%. Rodents were the only taxon trapped at Kamoamoā where 76 individuals were captured. Black rats comprised 62% of the capture, Polynesian rats 37%, and mice 1%.

## **Capture Rate**

There were differences in the capture rates of all species across habitats (Table 2). Populations of black rats (ANOVA,  $F_{4,16} = 6.93$ ,  $P = 0.002$ ) were highest in the Kīpuka Puauulu site. Polynesian rats (ANOVA,  $F_{4,16} = 13.93$ ,  $P \leq 0.001$ ) were equally common at the Kīpuka Puauulu and Lowland sites, mice were nearly absent in the ‘Ōla‘a sites and rare in the Lowlands. Norway rats were only trapped in the ‘Ōla‘a Forest sites; more were captured at the large tract compared to the small tract, but the difference was not significant (Kruskal-Wallis,  $P = 0.309$ )

### ***Mauna Loa Strip***

Although black rats were more common in the winter sessions (daily mean capture [SE]: 12.13 [3.22]) than in the summer (5.00 [1.36]), the difference was non-significant (Mann-Whitney U test,  $P = 0.051$ ). The difference in winter capture (0.69 [0.27]) versus summer (0.06 [0.06]) for Polynesian rats was also non-significant (Mann-Whitney U test,  $P = 0.056$ ). Mice were the only rodent group with a significant difference between winter (26.31 [5.34]) and summer (7.56 [2.07]) capture rates (Mann-Whitney U test,  $P = 0.003$ ). None of the species reached an asymptote in capture rates over the eight-day trapping period (Figure 8).

Although the average capture rate of black rats declined over the eight-day trapping period (Figure 9a), the difference was non-significant (Kruskal-Wallis  $P = 0.380$ ). Capture rates for Polynesian rats and mice did not follow a discernible pattern (Figure 9c, 9d).

### ***Kīpuka Puauulu***

The overall capture rate for rodents at Kīpuka Puauulu did not appear to be seasonally influenced. However, capture rates were higher in some trapping sessions than others: Polynesian rats were most numerous in the winter 1988 trapping period, and fewer mice were present in the summer 1988 and spring 1989 trapping sessions. None of the three rodent species reached an asymptote over the eight-day trapping period (Figure 10).

The capture rate for black rats significantly decreased over the eight-day trapping period (Kruskal-Wallis,  $P \leq 0.001$ ; Figure 9a), as did the number of Polynesian rats captured (Kruskal-Wallis,  $P = 0.022$ ; Figure 9c). There was no apparent trend in the capture rate of mice over the eight days of trapping (Figure 9d).

### ***‘Ōla‘a Large Tract***

There was no obvious seasonality in the capture rate for any of the three rat species at the ‘Ōla‘a Large Tract. Norway rats were very numerous in the summer 1986 trapping period but nearly absent in summer 1988 (Figure 11c). Black rats did not reach an asymptote during any of the trapping periods (Figure 11a). Norway rats reached asymptotes during all but the summer 1986 trapping period (Figure 11c). On the other hand, Polynesian rats reached asymptotes during all but the winter 1988 trapping period (Figure 11b).

More black rats were captured in the first days of trapping than in the later part of the sessions (Kruskal-Wallis,  $P = 0.001$ ; Figure 9a). The capture rates for Norway and Polynesian rats and mice did not differ significantly over the eight-day trapping period (Kruskal-Wallis,  $P$  always  $> 0.33$ ; Figure 9b, 9c).

### ***‘Ōla‘a Small Tract***

Black rats did not exhibit any obvious seasonality in abundance (Figure 12a) but Norway rats were most common in the winter (Kruskal-Wallis,  $P \leq 0.001$ ; Figure 12c). Although there were differences between the trapping sessions for Polynesian rats (significantly more common in the April 1988 trapping session, Kruskal-Wallis,  $P = 0.016$ ), differences in seasonality were not significant (Figure 12b).

The capture rate for both black (Kruskal-Wallis,  $P = 0.001$ ; Figure 9a) and Polynesian rats (Kruskal-Wallis,  $P = 0.023$ ; Figure 9c) significantly decreased over the eight-day trapping period while those of Norway rats and mice showed no obvious trends (Figure 9b).

### ***Lowlands (Nāulu and Kamoamo)***

None of the three species of rodent exhibited any significant seasonality in abundance as indicated by the capture rate (Figure 13). There was an average (SE) daily capture of 4.6 (1.5) black rats in the winter compared to 7.7 (2.1) in the spring, 6.7 (1.0) Polynesian rats in the winter and 7.1 (1.2) in the spring, and 2.4 (0.5) mice in the winter compared to 3.3 (0.6) in the spring. Black rats reached a near asymptote in all but the spring 1989 trapping session, but mice and Polynesian rats failed to reach an asymptote at any point.

Capture rate declined significantly over the eight-day trapping period for black rats ( $F_{7,20} = 15.79$ ,  $P \leq 0.001$ ; Figure 9a), and was higher in the first days for Polynesian rats as well ( $F_{7,20} = 36.05$ ,  $P \leq 0.001$ , log-transformed data; Figure 9c). Although there was a significant difference in capture rates between days ( $F_{7,20} = 7.42$ ,  $P \leq 0.001$ ) mice showed no apparent trend in capture rates over the eight-day trapping period (Figure 9d). None of the species showed significant differences in captures among the four sessions.

## **Age Structure**

### ***Mauna Loa Strip***

The median weight at maturity is presented in Table 3. There were generally more adult males trapped than sub-adult males for all species (Figure 14). In total, 70% of male black rats were adult (107 of 153 individuals) compared to 52% of females (64 of 122 individuals). Adult female black rats outnumbered sub-adults in the winter, but were captured in essentially equal numbers in the summer (Figure 14a). Polynesian rats were relatively rare in this environment: there were six adult males captured, no sub-adult males, and three each of adult and sub-adult females captured. Both adult and sub-adult female Polynesian rats were captured in equal numbers, regardless of season (Figure 14b). Adult male mice were much more likely to be captured – 78% of the total male capture (185 of 238 individuals) than sub-adults. For female mice, adults (52%, 124 of 238 individuals) and sub-adults were about equally likely to be captured. There was strong indication of seasonality in female mice at the Mauna Loa Strip: sub-adults were more common than adults in the winter and the reverse was true in the summer (Figure 14c).

### ***Kīpuka Puau***

With the exception of mice for which females were heavier, the median weight at maturity was greatest for male rodents (Table 3). There were more adult males trapped than sub-adult males and more sub-adult females than adults for all three rodent species. In total, 73% of captured

male black rats were adult (137 of 187 individuals) compared to 26% of females (43 of 164 individuals). There was some degree of seasonality in capture rates for adult and juvenile male black rats: adults outnumbered sub-adults in all seasons but fall; adult females were relatively less common throughout the year (Figure 15a). Sixty-one percent of male Polynesian rats were adult, compared to 35% of female Polynesian rats. Juvenile females outnumbered adults and adult males outnumbered sub-adults in all but the summer trapping periods (Figure 15b). Seventy-three percent of male mice were adult and 29% of female mice were adults. There were more subadult than adult females in all seasons except summer when numbers were similar (Figure 15c).

### ***‘Ōla‘a Forest Large Tract***

Except for Polynesian rats, female rats exhibited a greater weight at maturity than males (Table 3). Due to their rarity in this habitat, age structure for mice is not discussed further. Adult males were more common than sub-adults for all rat species and sub-adult females were more common than adults. In total, 89% (81 of 91 individuals) of captured male black rats were adults compared to only 34% of females (26 of 77 individuals). Adult male black rats were substantially more common than sub-adults in the winter, spring and summer, and sub-adult females were more common in the winter and summer but adult females were more common in the spring (Figure 16a). Eighty-nine percent of male Polynesian rats were adults (17 of 19 individuals), compared to only 25% of females (one of four individuals). Regardless of season, adult male Polynesian rats were always more common than sub-adult males; female Polynesian rats were only captured in the winter and spring trapping periods, and sub-adults were always more common than adults (Figure 16b). Sixty-seven percent of male Norway rats were adult (14 of 21 individuals) compared to 29% of female Norway rats (5 of 17 individuals). This species was only trapped in the spring and summer trapping periods and showed little seasonality in age structure. Like black and Polynesian rats, captured Norway males were substantially more likely to be adult than sub-adult, regardless of season and more sub-adult females were captured than adults in both trapping periods (Figure 16c).

### ***‘Ōla‘a Forest Small Tract***

As in the large tract, the median weight at maturity was greatest for female Norway and Black rats and for male Polynesian rats (Table 3). Due to their rarity, age structure for mice in this habitat is not discussed further. Adult male black rats always outnumbered sub-adult males and sub-adult females were always more common than adult females, regardless of season (Figure 17a). Adult black rats comprised 90% (138 of 153 individuals) of the male capture and 39% of the female capture (50 of 129 individuals). Adult Polynesian rats were almost always more common than sub-adults. As for black rats, adult males always outnumbered sub-adults with a total of 93% (81 of 87 individuals) of the male population being adult and 63% (43 of 68 individuals) being male; adult females were more common than sub-adults females in all but the winter season (Figure 17b). Norway rats were relatively rare in the small tract; adult males comprised 88% of the capture (seven of eight individuals) and adult females comprised 67% (two of three individuals). Males of this species showed some degree of seasonality: adults were more common in the winter and summer, and sub-adults in the spring trapping periods. Only three females were captured and it was not possible to speculate on seasonal trends, given this small sample size.

### ***Lowlands (Nāulu and Kamoamoa)***

Male rats had a higher median weight at maturity than females in the Lowlands (Table 3). Adults of all species were almost always more common than sub-adults in this habitat. Adult male black rats were more common than sub-adults (83% of the male population; 87 of 105 individuals), a trend that was particularly pronounced in the spring. Female adult (51%, 43 of 85 individuals) and sub-adult black rats were found in approximately equal proportions, however, adults outnumbered sub-adults in the winter and sub-adults outnumbered adults in the spring trapping periods (Figure 18a). Adult male Polynesian rats comprised 86% of the capture (108 of 125 individuals), while adult females comprised 58% (53 of 92 individuals). Adult males were substantially more common than sub-adults in both the winter and spring; adult females were slightly more common than sub-adults in the winter and occurred in approximately equal numbers in the spring (Figure 18b). Adult male mice outnumbered sub-adults (90% of the capture; 38 of 42 individuals) and adult females comprised 70% of the capture (28 of 40 individuals). Adults of both sexes were more common in both the winter and spring trapping sessions, but the trend was particularly pronounced for males in the spring (Figure 18c).

## **Female Reproduction**

### ***Mauna Loa Strip***

Reproductive female black rats and mice were more common in the summer than in the winter trapping periods (Figure 19a). The difference is statistically significant in mice (Kruskal-Wallis,  $P = 0.003$ ) but not in black rats due to a high variability in summer. Due to the low number of females captured, Polynesian rats were not included in these analyses.

There was a mean (SE) of 4.00 (0.24) embryos per pregnant black rat. Although the differences were not significant, black rats had more embryos per female in the summer than in the winter. Mice had an average of 3.83 (0.24) embryos per pregnant female and also had more in the summer months than in the winter, but again, this difference was not statistically significant.

### ***Kīpuka Puaulu***

Reproduction in females (pregnant or lactating individuals) occurred throughout the year. There were no seasonal differences in the percent of the total females that were reproductive for mice (Kruskal-Wallis,  $P = 0.072$ ), or black rats (Kruskal-Wallis,  $P = 0.170$ ), but there was a significant decrease in the percentage of Polynesian rat females who were reproducing in the winter and spring (Kruskal-Wallis,  $P = 0.023$ , Figure 19b).

Black rats had a mean (SE) of 3.75 (0.65) embryos per pregnant female, Polynesian rats had 4.0 (0.57) and mice had 4.5 (0.71). Although the differences were not significant, black rats and mice had more embryos in the summer, and Polynesian rats had more in the spring; there were no pregnant black rats in the fall and no pregnant rodents of any species in the winter.

### ***‘Ōla‘a Forest Large Tract***

A larger percentage of the female black rat population was reproductive during the spring than during the winter; reproductive Polynesian rats were only trapped during the winter. Norway rats were not trapped during the winter, but females were found to be reproductive during spring and summer, the only seasons when they were captured (Figure 19c). There were no differences

in the percent of females that were reproductive across seasons for any of the three species of rats (Kruskal-Wallis,  $P$  always  $\geq 0.276$ ).

Pregnant black rats ( $n = 12$ ) had an overall mean (SE) of 4.83 (3.67) embryos and had significantly more embryos in the summer (5.5 [0.27]) than in the spring (3.5 [0.50], Kruskal-Wallis  $P = 0.012$ ). The two pregnant Norway rats (captured in the spring and summer) and single Polynesian rat (captured in the winter) each had 4 embryos.

### ***‘Ōla‘a Forest Small Tract***

Reproduction occurred throughout the year for black and Polynesian rats and there were no significant differences in the percent of the female population that was pregnant or lactating across seasons (Figure 19d). Because of the very low number of female Norway rats ( $n = 3$ ), this species is not considered in the following analysis.

Black rats had significantly more (mean (SE) of 4.5 (0.26)) embryos per pregnant female than Polynesian rats (3.4 (0.26), Kruskal-Wallis,  $P = 0.003$ ). There were no significant seasonal differences for either species in the number of embryos.

### ***Lowlands (Nāulu and Kamoamo)***

There was no significant difference between winter and spring for any of the three species of rodents in terms of the percentage of the female population that was actively reproductive (Figure 19e).

Black rats had a mean (SE) of 3.57 (0.33) embryos per female, Polynesian rats had 3.65 (0.31) and mice 3.92 (0.47); the differences between species were slight and non-significant. None of the three species exhibited seasonal differences in the mean number of embryos per female.

## **Sex Ratio**

### ***Mauna Loa Strip***

Over all seasons black rats had a ratio of 1.2 males per female ( $n = 304$ ), which did not significantly differ from a 1:1 ratio (chi-square test). There were no significant differences in the sex ratio for any of the trapping periods, nor was there any distinct difference between winter and summer in sex ratio (Figure 20a).

Polynesian rats were relatively rare in this environment, and chi-square tests were not performed on the data. Overall, six males and five females were captured. Two males and one female were captured in the summer trapping periods; four males and four females were captured in the winter trapping periods.

Mice exhibited an overall sex ratio of 0.88:1 males:females, which did not significantly differ from a 1:1 ratio. Females were significantly more common in the summer trapping periods (ratio = 0.75:1,  $n = 199$ ,  $\chi^2 = 4.23$ ,  $P = 0.040$ ; Figure 20a).

### ***Kīpuka Puaulu***

Black rats had an overall ratio of 1.2 males per female ( $n = 351$ ), but this was not significantly different from the expected 1:1 ratio (chi-square tests). Fluctuations in sex ratio over the seasons occurred, but the differences were not significant (Figure 20b).

Overall sex ratio in Polynesian rats was significantly male-biased (1.4 males per female,  $n = 248$ ,  $\chi^2 = 6.21$ ,  $df = 1$ ,  $P = 0.013$ ); this male bias was particularly pronounced in the summer 1988 trapping period when a 2:1 ratio was observed ( $\chi^2 = 5.00$ ,  $df = 1$ ,  $P = 0.025$ ).

Mice populations also exhibited a male-biased sex ratio. Although in the summer the sex ratio was nearly 1:1, the overall ratio was 1.6 males per female ( $\chi^2 = 10.60$ ,  $df = 1$ ,  $P = 0.037$ ); this was particularly pronounced in the winter 1988 (2.5:1,  $\chi^2 = 11.27$ ,  $df = 1$ ,  $P = 0.001$ ) and fall 1989 (1.78:1,  $\chi^2 = 3.92$ ,  $df = 1$ ,  $P = 0.048$ ) trapping periods.

### ***‘Ōla‘a Forest Large Tract***

The overall sex ratio for black rats was 1.2 males per female ( $n = 168$ ); this ratio did not significantly differ from a 1:1 ratio. Seasonal (winter, spring, summer) differences in black rat sex ratio (Figure 20c) were not significant.

Norway rats had an overall sex ratio of 1.2 males per female ( $n = 38$ ), which did not significantly differ from a 1:1 ratio. The sex ratio of Norway rats did not appear to be seasonally influenced (Figure 20c). No Norway rats were trapped in the winter trapping period. In the spring the sex ratio was 1.3:1 ( $n = 9$ ) and in the summer it was 1.2:1 ( $n = 29$ ).

Polynesian rats had an overall ratio of 4.8 males per female, a ratio which differed significantly from a 1:1 ratio ( $\chi^2 = 9.78$ ,  $n = 23$ ,  $P = 0.002$ ). Males were trapped in all three trapping periods, but no females were captured in the summer (Figure 20c). Sex ratio was 3.3:1 in the winter ( $\chi^2 = 3.77$ ,  $n = 13$ ,  $P = 0.052$ ) and 4:1 in the spring (NS,  $n = 5$ ).

### ***‘Ōla‘a Forest Small Tract***

Although the sex ratio for rats at the ‘Ōla‘a Small Tract was slightly male-biased (Figure 20d), it did not significantly differ from a 1:1 ratio for any species or during any trapping period or season. Black rats had an overall ratio of 1.2 males per female ( $n = 282$ ), Polynesian rats 1.3 males per female ( $n = 155$ ), and Norway rats 2.7 males per female ( $n = 11$ ).

### ***Lowlands (Nāulu and Kamoamo)***

Overall, there were no significant differences in the sex ratio for any of the three rodent species collected in the Lowlands (Figure 20e); rats were slightly male-biased (1.2:1 for black and 1.6:1 for Polynesian) and mice of both sexes were equally common. There were no differences in the spring trapping periods, but in the winter, there were significantly more male Polynesian rats than females (1.5:1,  $\chi^2 = 3.85$ ,  $P = 0.050$ ; Figure 20e). Although the differences in sex ratio for mice seemed substantial, they were not significant.

### **Size**

Using weight as a proxy for overall body size, black rats were largest in the small tract at ‘Ōla‘a Forest and smallest in the Lowlands and Mauna Loa Strip (ANOVA,  $F_{4,1196} = 26.5$ ,  $P \leq 0.001$ , Figure 21a). Polynesian rats were largest in ‘Ōla‘a Forest and similar in size in the Mauna Loa



Strip, Kīpuka Puauulu, and lowland sites (ANOVA,  $F_{4,595} = 19.6$ ,  $P \leq 0.001$ , Figure 21b). There was no significant difference in the size of Norway rats in the two ‘Ōla‘a Forest sites, the only areas where this species occurred (Figure 21c). Mice were largest in the Mauna Loa strip and smallest at Kīpuka Puauulu  $F_{2,718} = 5.7$ ,  $P = 0.004$ , Figure 21d).

## **Movement Patterns**

Analysis of movement patterns was not possible for all sites due to low sample sizes. In some locations only very few of the rodents captured had fluorescent dye in their stomachs: 3 of 835 at the Mauna Loa strip, 13 out of 821 at Kīpuka Puauulu, and 12 of 235 at the ‘Ōla‘a Large Tract.

### ***‘Ōla‘a Forest Small Tract***

Forty-two individuals of three species had eaten the fluorescent dye from the movement assessment line (Table 4). The mean minimum distance traveled by Norway rats was greater than that of either Polynesian rats or black rats (ANOVA,  $F_{39,2} = 9.741$ ,  $P \leq 0.001$ ). There was no significant seasonality in distance traveled for any of the three species (Figure 22). Black and Polynesian rats traveled farther in the spring trapping period (ANOVA,  $P$  always  $\geq 0.223$ ). Norway rats were only captured in the summer and winter periods and traveled farther in the summer than winter months (ANOVA,  $F_{2,1} = 12.332$ ,  $P = 0.072$ ).

### ***Lowlands (Nāulu and Kamoamo)***

Twenty-one of 433 individual rodents from Nāulu were found to have dye in their stomachs. A single mongoose also had dye but was not included in the following analysis. No dye was present for any of the captures from Kamoamo. Black rats traveled substantially larger distances than did Polynesian rats although the results were non-significant, possibly due to small sample size (Kruskal-Wallis,  $P = 0.059$ ; Table 4). Black rats with dye present were only captured in the winter trapping periods. Polynesian rats traveled farther in the winter (mean [SE] = 82.20 [30.28] m) than spring (23.88 [5.01] m) months but the difference was not great, nor was it significant (Kruskal-Wallis,  $P = 0.123$ ).

## **Pelage Color**

### ***Mauna Loa Strip***

Overall, black was the most common color morph at the Mauna Loa Strip site. Of the 267 rats for which pelage color was recorded (no pelage color was recorded for eight individuals), 32% ( $n = 85$ ) were agouti white (AW), nearly half (46%,  $n = 124$ ) were black (B), and the remaining 22% ( $n = 58$ ) were agouti grey (AG). This AW:B:AG ratio of 1.5:2.1:1 was significantly different from a 1:1:1 ratio ( $\chi^2 = 24.74$ ,  $P \leq 0.001$ ). The trend was strongest in the summer trapping months ( $\chi^2 = 27.67$ ,  $P \leq 0.001$ ), but was evident in the winter as well ( $\chi^2 = 7.45$ ,  $P = 0.024$ ) (Figure 23a).

### ***Kīpuka Puauulu***

Pelage color was not recorded for black rats during the winter (February-March 1988) field season. In the spring, summer and fall, agouti white was the most common color morph at Kīpuka Puauulu, occurring in 46% of the captured individuals. Black pelage occurred in 35% of the individuals and agouti grey in only 19%. This AW:B:AG ratio of 2.4:1.8:1 was significantly different from a 1:1:1 ratio ( $\chi^2 = 31.938$ ,  $P \leq 0.001$ ). The trend towards more agouti white and

black individuals than grey was most pronounced in the summer, but continued throughout the portion of the year in which it was recorded (Figure 23b).

### ***'Ōla'a Large Tract***

Overall, black was the most common color morph in the 'Ōla'a Large tract. Only 2% had agouti white coats, 88% of all recorded (color was not recorded for two of the 169 black rats captured) individuals had black pelage and 10% were agouti grey. The ratio of agouti white:black:agouti grey was 1:36.8:4 which was significantly different from a 1:1:1 ratio ( $\chi^2 = 226.07$ ,  $n = 167$ ,  $P \leq 0.001$ ). There was a significantly larger proportion of the population with black coats and fewer with agouti grey coats year-round, but this trend was particularly noticeable in the spring trapping periods (Figure 23c).

### ***'Ōla'a Small Tract***

Overall, black was the most common color morph for black rats in the 'Ōla'a Small Tract. Agouti white rats comprised 15% ( $n = 41$ ) of the rats captured, black rats 65% ( $n = 178$ ), and agouti grey 20% ( $n = 55$ ). This ratio of 1:4.3:1.3 was significantly different from a 1:1:1 ratio ( $\chi^2 = 124.4$ ,  $P \leq 0.001$ ). There were significantly more black rats during all seasons of trapping, but agouti white was relatively more common and agouti grey less common in the winter trapping period (Figure 23d).

### ***Lowlands (Nāulu and Kamoamo)***

Overall, agouti white (38%,  $n = 69$ ) and black (42%,  $n = 76$ ) occurred in nearly equal proportions while agouti grey (21%,  $n = 38$ ) was a substantially less common color morph for black rats caught in the Lowlands. This AW:B:AG ratio of 1.8:2:1 was significantly different from a 1:1:1 ratio ( $\chi^2 = 13.41$ ,  $P = 0.001$ ). Black and agouti white rats were about equally common at the Nāulu site with an AW:B:AG ratio of 2.4:2.1:1 ( $\chi^2 = 14.22$ ,  $P = 0.001$ ), but black rats were by far the most common morph at Kamoamo 1:2.4:1.3 ( $\chi^2 = 6.94$ ,  $P = 0.031$ ). The differences in pelage color were not noticeable in the winter trapping months, but black and agouti white were markedly more common in the spring trapping periods ( $\chi^2 = 11.66$ ,  $P = 0.003$ , Figure 23e).

## **DISCUSSION**

Rodent species composition in Hawai'i Volcanoes National Park is strongly influenced by location. In the high elevation Mauna Loa Strip study site, mice comprised a substantial majority of the rodent species captured. At moderately high elevations, mice are known to have a diet comprised mostly of seeds (both monocot and dicot) and invertebrates; black rats eat mostly fruits, vegetative plant matter and invertebrates (Sugihara 1997, Cole et al. 2000) and the Polynesian rat diet is primarily composed of invertebrates (Sugihara 1997). The vegetation of the Mauna Loa Strip area is predominantly composed of shrubby small-seeded plants and grasses (Doty and Mueller-Dombois 1966), which would provide the ideal diet for mice, but perhaps not enough large fleshy fruits to sustain a large population of black rats. There is also some indication that Polynesian rats are negatively influenced by the presence of mice (Yom-Tov et al. 1999), perhaps because of the dependence of both species on invertebrates as a food source (Sugihara 1997, Cole et al. 2000). The Mauna Loa Strip site is the only area where Polynesian rats comprise less than 10% of the total capture and the only area where mice comprise more than 30% (Figure 7a).

At the Kīpuka Puauolu site, black rats, Polynesian rats, and mice were approximately evenly represented in the rodent community (Figure 7b). Two distinct vegetation communities are found at Kīpuka Puauolu: montane mesic forest and savanna with dense grass cover and occasional trees (Mueller-Dombois and Lamoureux 1967). The heterogeneity of the environment has the potential to provide resources for all three rodent species: a large quantity of monocot seeds as well as a variety of forest trees and other plants that produce fruits known to be eaten by rats, such as blackberry (*Rubus argutus*), pilo (*Coprosma rhynchocarpa*), pāpala kēpau (*Pisonia brunoniana*), and hō‘awa (*Pittosporum hosmeri*) (e.g., Mueller-Dombois and Lamoureux 1967, Sugihara 1997, Spurr et al. 2003). The diversity of vegetation would also be expected to provide habitat for a diverse arthropod community.

In the wet forest (‘Ōla‘a), black rats were clearly the dominant rodent species, comprising over 70% of the capture in both the Large and Small Tracts (Figure 7c, 7d). Proportions of black, Polynesian, and Norway rats are similar to those found in other studies conducted in montane Hawaiian forests (Lindsey et al. 1999). Forest trees provide a large quantity of fleshy fruits and habitat suitable for the arboreal nature (Marsh 1994) of black rats. Mice were nearly absent in this habitat, perhaps because of the lack of monocot seeds in the forest, or perhaps because of competitive interactions between mice and black rats (Ruscoe 2001). It is interesting to note that in similar habitat—though at somewhat higher elevations at Hanawī Preserve on Maui—numbers of mice captures were similar to captures of black rats and Polynesian rats (Sugihara 1997). Norway rats were more common in the large tract compared to the small tract at ‘Ōla‘a Forest and this may be due to differences in surrounding land use. At the time of the study, the cattle ranch immediately adjacent to the large tract was in active use, and structures such as barns were present. Norway rats are often closely associated with humans and usually found in anthropogenic settings near buildings and man-made animal shelters (Timm 1994b, Nogales et al. 2006), so it is not surprising to find them in larger numbers in areas located closer to human activity. Norway rats are known to prey on both Polynesian rats and mice (Moors 1990). The ‘Ōla‘a Forest sites were the only ones where Norway rats were present, and at both sites mice were nearly absent. In the large tract, where Norway rats were more numerous, Polynesian rats were present in reduced proportions compared to sites where Norway rats were absent or rare. These results suggest a matrix of potential interspecific interactions among park rodents that deserve further attention.

The lowland sites were the only sites where Polynesian rats were the dominant rodent species. Polynesian rats are generally more numerous at lower elevations (Tomich 1981, Tobin 1994). Although they are known to be commensal with humans, in Hawai‘i they are often found in areas that are removed from human habitation (Tobin 1994). Their diet consists of arthropods (Sugihara 1997) and fleshy fruits (Tobin 1994), both of which were quite common in this habitat.

Weight was highest for both Black rats and Polynesian rats in the mid-elevation ‘Ōla‘a sites (Figure 21), the only site where Norway rats were also captured. These wet forest sites contain a diverse array of fruit-producing plants, nesting birds, and insects, and appear to be optimum habitat for rodents that can exploit the wide range of food items. However, rats of both sexes in this habitat were, on average, larger at sexual maturity than rats in the two sites at the extreme of the elevation gradient (Mauna Loa Strip and the Lowlands, Table 3). Because weight is a good

index of age in rodents (Davis 1953), this suggests that maturation may be somewhat delayed at the wet forest mid-elevation sites ('Ōla'a Forest). An alternative possibility is that young rodents are gaining weight more quickly in these sites. It is interesting to note that both average weight and the median weight at maturity for rodents at all HAVO sites is substantially larger than that recorded on the island of O'ahu by Tamarin and Malecha (1971). It may be that high productivity of these Hawai'i Island sites results in increased overall weight gain and allows rodents to delay maturity and still maintain population sizes. The mean number of embryos per female was noticeably higher in the 'Ōla'a sites than in the other three sites, and it appears that any delay in maturation is being compensated for to some extent by increased fecundity. The number of embryos per female for black rats fell within the range of values encountered in other Hawai'i Island sites (Tobin et al. 1994).

In contrast to the trends for rats, the median size at maturity of male mice was larger in the sites at the elevation extremes (Mauna Loa Strip and the Lowlands), and female mice were larger at maturity in the Kīpuka Puaulu site.

We noted little seasonality in the abundance of rodents in Hawai'i Volcanoes National Park. The one exception to this trend was at the Mauna Loa Strip site, our highest elevation site. All three species of rodents (black and Polynesian rats, and mice) were trapped in larger numbers in the winter trapping periods than in the summer. At the small tract of 'Ōla'a Forest, we captured more Norway rats in the winter than in the summer, but Norway rats were captured in low numbers during both 'Ōla'a trapping periods, so this may be an artifact of the data. Increases in rodent populations have been shown to be correlated with rainfall patterns (and related increases in food supply) and the abundance of natural enemies (Korpimäki 2004). These factors were not examined in this study but could have contributed to the abundance patterns at these sites.

Reproduction appeared to occur throughout the year at all sites. However, based on the number of reproductive females and the number of sub-adult captures, it is likely that there were seasonal peaks in reproduction. Year-round reproduction punctuated by seasonal peaks is common in Hawaiian rodent populations (Tamarin and Malecha 1971, Tobin et al. 1994, Lindsey et al. 1999), although seasonality has been reported in some populations (Wirtz II 1972, Sugihara 1997). Seasonal peaks in reproduction were particularly noticeable in our higher elevation sites (Mauna Loa Strip and, to a lesser extent, Kīpuka Puaulu). In both of these sites females of at least one rodent species were more likely to be actively reproducing in the summer trapping periods than in the winter. At Mauna Loa Strip, this was particularly evident in mice, although reproductive female black rats were also somewhat more common in the summer. Sub-adults were more common in the winter, which may be due to a time lag between pregnancy and movement patterns of juveniles. At Kīpuka Puaulu, there were fewer reproductive females of all three species in the winter, although the differences were only significant for Polynesian rats. Sub-adult Polynesian rats were most common in the winter although there was also a small peak in the summer trapping periods. Sub-adult mice were most common in the fall and winter, although sub-adult black rats were most common in the summer. Although the differences in the capture rate of reproductive females was not significant in either site, there were some indication of seasonality among reproductive females at the two 'Ōla'a Forest sites. Polynesian rats exhibited a bi-modal reproductive pattern: high numbers of reproductive females in both the summer and winter, but low in the spring. Black and Norway rats were more likely to be

reproductive in the spring than in either summer or winter and juveniles were most common in the summer. In the Lowlands, trapping was not conducted in the summer and it is difficult to predict what the actual trend might be. However, unlike the higher elevation sites, reproductive female rats were somewhat more common in the winter than in the spring, and sub-adults were more common in the spring, indicating a winter birth. Thus, in the higher elevation sites, reproduction appeared to be primarily occurring in the warmest months, and in the lower elevation (warmer) sites it appears to be at its peak in the cooler months. The more temperate wet forest sites had an intermediate pattern with reproduction peaking in the spring (intermediate between the warmest and coolest trapping seasons) for black and Norway rats and bimodal peaks in reproduction (occurring in both the warmest and coolest periods) for Polynesian rats.

The sex ratio for black and Norway rats did not significantly differ from a 1:1 ratio at any of the sites, a pattern found for many populations of black rats living in non-agricultural environments (Clark 1980). Polynesian rats exhibited a male-biased sex ratio at both Kīpuka Puauulu and at the large tract in 'Ōla'a Forest and seasonal differences in sex ratio in the Lowlands. In all cases, this trend was most evident during the months when reproductive females were most common. This was the case in the summer in Kīpuka Puauulu, summer and winter in 'Ōla'a Forest, and winter in the Lowlands. When females are actively reproductive, male rats may be ranging further in search of females and thus be more likely to be trapped. In contrast, pregnant females may be ranging less and thus be less trappable.

The sex ratio of mice exhibited the opposite trend in relation to female reproduction than that of Polynesian rats. Male mice were trapped in significantly larger numbers than females in the winter at both the Mauna Loa Strip and Kīpuka Puauulu sites and in the fall at Kīpuka Puauulu (no data were collected in fall months at the Mauna Loa Strip). Females were more common than males in the summer at the Mauna Loa Strip. Although there were no significant seasonal differences in the proportion of reproductive females captured, there were generally proportionally fewer in the winter at all of the study sites. In New Zealand, actively reproductive female mice have been found to travel longer-distances than males or non-pregnant/lactating females (Ruscoe 2001). There were no significant differences in the sex ratio of mice in lower-elevation sites during any season.

Due to the small number of captured individuals which contained the marker, it is difficult to assess movement patterns for the different rodent species. Although it appears that black rats travel farther in the Lowlands than in the wet forest (Table 4), variation is high and it is impossible to say whether actual differences in the distance traveled exist between these sites. Daily movement patterns in rodents are quite variable. For example, although mice are generally known for relatively limited (<9 m) movement patterns (Timm 1994a) they have the ability to travel substantial distances (>150 m) between captures (Ruscoe 2001). Not surprisingly, rodent body size appears to play a role in movement patterns: Norway rats, the largest of the rodent species studied here, exhibited significantly larger minimum distances traveled in the 'Ōla'a forest than either black or Polynesian rats. In the absence of con-specific competition, Norway rats are known to have large home ranges and can disperse over large distances (Russell et al. 2005).

In general, black was the most common pelage color in black rats although agouti white was common in the drier sites (Figure 23). Pelage color may have adaptive value both for avoiding predation and for thermoregulation. For example, in Galápagos, darker-colored black rats are found in areas with darker soil and more shadows (Clark 1980). However, Tomich found no apparent patterns in a survey of pelage color across Hawai'i Island. Our results indicate that rats were darker in Hawaiian forests, while lighter-colored individuals are more common in open habitat.

## CONCLUSIONS

Rodent populations in Hawai'i Volcanoes National Park varied by location, environment, and season. They occurred in a broad range of habitats. Mouse populations were comparatively greater in higher elevation sites, and Polynesian rats comprised the largest proportion of the rodents found in low elevation sites. Black rats were numerous in all surveyed habitats. Like previously published studies (e.g., Tamarin and Malecha 1971, Tobin et al. 1994) we found that introduced Hawaiian rodents undergo yearly reproductive cycles, but that some degree of reproductive activity occurred year-round. Cyclic fluctuations in abundance were rare in all but our highest elevation site, which had the largest seasonal variation in temperature.

This study was conducted across a range of Hawaiian plant communities which encompass a variety of associated avian and arthropod species. The full impact of introduced rodents on Hawaiian biodiversity is still poorly understood, but it is clear that they negatively affect plants (Russell 1980, Male and Loeffler 1997, Cabin et al. 2000, Cole et al. 2000), arthropods (Sugihara 1997, Cole et al. 2000), and birds (Tomich 1969, Atkinson 1977, Berger 1981, Amarasekare 1993, Levy 2003). Effective rodent control is an important factor in native species protection in Hawai'i. Despite their prevalence throughout the state, there are still large gaps in our understanding of the basic biology of introduced rodents in Hawai'i. Understanding the species-specific ecology of this group is critical to our ability to design effective programs for control and to prevent or decrease the damage rodents cause to native ecosystems and species.

Lindsey et al. (1999) state that rodent control programs are most successful when they are conducted so that they coincide with natural population fluctuations. Although seasonal fluctuations in abundance were rare in our study areas, an effective control program could be centered about seasonal peaks in reproductive activity, keeping bait stations well-within the natural distances traveled by the targeted species. Other researchers have found that in areas where multiple species are found, the more dominant black and Norway rats are trapped in the first couple of days, then Polynesian rats are caught (R. Sugihara, USDA, pers. comm.). In this study we found high initial capture rates for all rat species; this rate declined after the first 3-5 days. However, the same trend did not hold true for mice, and a longer trapping period would be needed to effectively control this species.

Recent research on endangered Hawaiian plants in Hawaii Volcanoes National Park has documented the impact of rodents on seeds (Pratt et al. 2011). Broad-area ground-based control programs utilizing baits with 0.005% Diphacinone have been tested to protect the Po'ouli (*Melanprosops phaeosoma*), an endangered Hawaiian honeycreeper now believed to be extinct on Maui (Malcolm et al. 2008), and efficacy trials for aerial application of similar baits have been conducted in Hawaii Volcanoes National Park (Spurr et al. 2003). Data on both historical

and contemporary ecology of rodents are important for developing large area control programs to protect native Hawaiian ecosystems (Drake and Hunt, 2009). This study provides historical information on the ecology and distribution of introduced rodents in Hawaii Volcanoes National Park and, by doing so, provides a foundation for future studies and rodent control programs conducted in the park and elsewhere.

### **ACKNOWLEDGMENTS**

We are grateful to S. Anderson, S. Fellows, P. Higashino, L.W. Pratt, G. Santos, D. Stone, and J. Yoshioka of the former Research Division at Hawai'i Volcanoes National Park for assistance collecting rats from the field and processing them in the laboratory. We greatly appreciate additional assistance from L.W. Pratt locating original project notes and maps and preparing the study site description. V. Doan prepared the final study area maps with site details. K. Magnacca and C. Cooper assisted with troubleshooting computer programs. Helpful comments on drafts of the manuscript were provided by D. Duffy, S. Hess, L.W. Pratt, E. Spurr, R. Sugihara and L. Tango. This analysis of historical data was made possible in part thanks to support from the National Park Service Inventory and Monitoring Program and the U.S. Geological Survey Invasive Species Program. The authors would like to acknowledge additional support from the Pacific Cooperative Studies Unit, University of Hawai'i at Mānoa. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## LITERATURE CITED

- Abdelkrim, J., M. Pascal, C. Calmet, and S. Samadi. 2004. Importance of assessing population genetic structure before eradication of invasive species: Examples from insular Norway rat populations. *Conservation Biology* **19**:1509-1518.
- Allen, W. 2000. Restoring Hawaii's dry forests. *Bioscience* **50**:1037-1041.
- Amarasekare, P. 1993. Potential impact of mammalian nest predators on endemic forest birds of western Mauna Kea, Hawaii. *Conservation Biology* **7**:316-324.
- Athens S.J. 2009. *Rattus exulans* and the catastrophic disappearance of Hawai'i's native lowland forest. *Biological Invasions* **11**:1489–1501
- 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. *Pacific Science* **31**:109-133.
- Beauvais, G. P., and S. W. Buskirk. 1999. Modifying estimates of sampling effort to account for sprung traps. *Wildlife Society Bulletin* **27**:39-43.
- Berger, A. J. 1981. Hawaiian birdlife. 2nd edition. University Press of Hawaii, Honolulu.
- Cabin, R. J., S. G. Weller, D. H. Lorence, T. W. Flynn, A. K. Sakai, D. Sandquest, and L. J. Hadway. 2000. Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration of a Hawaiian tropical dry forest. *Conservation Biology* **14**:439-453.
- Clark, D. A. 1981. Foraging patterns of black rats across a desert-montane forest gradient in the Galápagos Islands. *Biotropica* **13**:182-194.
- Clark, D. B. 1980. Population ecology of *Rattus rattus* across a desert-montane forest gradient in the Galápagos Islands. *Ecology* **61**:1422-1433.
- Cole, F. R., L. L. Loope, A. C. Medeiros, C. E. Howe, and L. J. Anderson. 2000. Food habits of introduced rodents in high-elevation shrubland of Haleakalā National Park, Maui, Hawai'i. *Pacific Science* **54**:313-329.
- Davis, D. E. 1953. The characteristics of rat populations. *The Quarterly Review of Biology* **28**:373-401.
- Davis, D. E. 1956. Manual for analysis of rodent populations. The Pennsylvania State University, University Park.
- Delgado García, J. D., J. R. Arévalo, and J. M. Fernández-Palacios. 2005. Patterns of artificial avian nest predation by introduced rats in a fragmented laurel forest (Tenerife, Canary Islands). *Journal of Natural History* **38**:2661-2669.
- Diamond, J. M., and C. R. Veitch. 1981. Extinctions and introductions in the New Zealand avifauna: Cause and effect? *Science* **211**:499-501.
- Doty, M. S. and D. Mueller-Dombois. 1966. Atlas for bioecological studies at Hawaii Volcanoes National Park. Hawaii Botanical Science Paper No. 2. 507 pp.
- Drake, D. R., T. L. Hunt. 2009. Invasive rodents on islands: integrating historical and contemporary ecology. *Biological Invasions* **11**:1483–1487
- Fukami, T, D. A. Wardle, P. J. Bellingham, C. P. H. Mulder, D. P. Towns, G. W. Yeates, K. I. Bonner, M. S. Durrett, M. N. Grant-Hoffman, W. M. Williamson. 2006. Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. *Ecology Letters* **9**:1299–130
- Ganzhorn, J. U. 2003. Effects of introduced *Rattus rattus* on endemic small mammals in dry deciduous forest fragments of western Madagascar. *Animal Conservation* **6**:147-157.
- Gorresen, P. M., R. J. Camp, M. H. Reynolds, B. L. Woodworth, and T. K. Pratt. 2009. Status and trends of native Hawaiian songbirds. Chapter 5 in T.K. Pratt, C.T. Atkinson, P.



- Banko, J. Jacobi, and B.L. Woodworth, eds. Conservation Biology of Hawaiian Forest Birds: Implications for island avifauna. Yale University Press, New York, U.S.A.
- Harper, G. A., K. J. M. Dickenson, and P. J. Seddon. 2005. Habitat use by three rat species (*Rattus* spp.) on Steward Island/Rakiura, New Zealand. *New Zealand Journal of Ecology* **29**:251-260.
- Holcomb, R. T. 1987. Eruptive history and long-term behavior of Kilauea Volcano. Pages 261-350 in R. W. Decker, T. L. Wright, and P. H. Stauffer, editors. *Volcanism in Hawaii*. U.S. Geological Survey Professional Paper 1350, Washington, DC.
- Hollingsworth, R. G., R. Kaneta, J. J. Sullivan, H. S. Bishop, Y. Qvarnstrom, A. J. da Silva and D. G. Robinson 2007 Distribution of *Parmarion* cf. *martensi* (Pulmonata: Helicarionidae), a new semi-slug pest on Hawai'i Island, and its potential as a vector for human angiostrongyliasis. *Pacific Science* **61**:457-467
- Jones, H. P., R. Williamhenry III, G. R. Howald, B. R. Tershy, and D. A. Croll. 2006. Predation of artificial Xantus's murrelet (*Synthliboramphus hypoleucus scrippsi*) nests before and after black rat (*Rattus rattus*) eradication. *Environmental Conservation* **32**:320-325.
- Kirch, P. 1982. The impact of the prehistoric Polynesians on the Hawaiian ecosystem. *Pacific Science* **36**:1-14.
- Korpimäki, E., P. R. Brown, J. Jacob, and R. P. Pech. 2004. The puzzles of population cycles and outbreaks of small mammals solved? *BioScience* **54**:1071-1079.
- Levy, S. 2003. Getting the drop on Hawaiian invasives. *Bioscience* **53**:694-699.
- Lindsey, G. D., S. M. Mosher, S. G. Fancy, and T. D. Smucker. 1999. Population structure and movements of introduced rats in an Hawaiian rainforest. *Pacific Conservation Biology* **5**:94-102.
- Lockwood, J. P., P. W. Lipman, and F. R. Warshauer. 1988. Generalized ages of surface lava flows of Mauna Loa Volcano, Hawaii. U.S. Geological Survey, Denver.
- Major, H. L., and I. L. Jones. 2005. Distribution and prey selection of the introduced Norway Rat *Rattus norvegicus* at Kiska Island, Aleutian Islands, Alaska. *Pacific Conservation Biology* **11**:105-113.
- Malcolm, T. R., K. J. Swinnerton, M. J. Groombridge, W. D. Sparklin, C. N. Brosius, J. P. Vetter and J. T. Foster. 2008. Ground-based rodent control in a remote Hawaiian rainforest on Maui. *Pacific Conservation Biology* **14**:206-214.
- Male, T., and W. Loeffler. 1997. Patterns of distribution and seed predation in a population of *Prichardia hillebrandii*. *Newsletter of the Hawaiian Botanical Society* **36**:1-10.
- Marsh, R. 1994. Roof rats. Pages 125-132 in S. E. Hygnstrom, R. M. Timm, and G. E. Larson, editors. *Prevention and Control of Wildlife Damage*. University of Nebraska, Lincoln.
- Mooney, H. A., and R. J. Hobbs, editors. 2000. *Invasive species in a changing world*. Island Press, Washington, DC.
- Moors, P. J. 1990. Norway rat. Pages 192-206 in C. M. King, editor. *The handbook of New Zealand mammals*. Oxford University Press, Auckland.
- Mueller-Dombois, D., and C. H. Lamoureux. 1967. Soil-vegetation relationships in Hawaiian kipukas. *Pacific Science* **21**:286-299.
- Meyer, W.M. and A.B. Shiels. 2009. Black rat (*Rattus rattus*) predation on non-indigenous snails in Hawaii: complex management implications. *Pacific Science* **63**(3):339-347
- Nogales, M., J. L. Rodríguez-Luengo, and P. Marrero. 2006. Ecological effects and distribution of invasive non-native mammals on the Canary Islands. *Mammal Review* **36**:49-65.

- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* **52**:273-288.
- Pratt, L. W., and L. L. Abbott. 1997. Rare plants within managed units of 'Ola'a Forest, Hawaii Volcanoes National Park. 115, Cooperative National Park Resources Studies Unit, University of Hawaii at Manoa, Honolulu.
- Pratt, L. W., J. R. VanDemark, and M. Euaparadorn. 2011. Status and limiting factors of three rare plant species in the lowlands and mid-elevation woodlands of Hawaii Volcanoes National Park. Hawaii Cooperative Studies Unit Technical Report HCSU-024. University of Hawaii at Hilo. 89 pp.
- Ruscoe, W. A. 2001. Advances in New Zealand mammalogy 1990-2000: House mouse. *Journal of the Royal Society of New Zealand* **31**:127-134.
- 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 of the Third Conference in Natural Science*. Cooperative National Park Resources Studies Unit/University of Hawaii at Manoa, Hawaii Volcanoes National Park.
- Russell, J. C., D. R. Towns, S. H. Anderson, and M. N. Clout. 2005. Intercepting the first rat ashore. *Nature* **437**:1107.
- Shiels, A.B. 2011. Frugivory by introduced black rats (*Rattus rattus*) promotes dispersal of invasive plant seeds. *Biological Invasions* **13**:781-792
- Shiels, A.B. and D.R. Drake. 2011. Are introduced rats (*Rattus rattus*) both seed predators and dispersers in Hawaii? *Biological Invasions* **13**:883-894.
- Simberloff, D. 2009. Rats are not the only introduced rodents producing ecosystem impacts on islands. *Biological Invasions* **11**:1735-1742
- Smith, D. G., E. K. Shiinoki, and E. A. VanderWerf. 2006. Recovery of native species following rat eradication on Mokoli'i Island, O'ahu, Hawai'i. *Pacific Science* **60**:299-303.
- Spurr, E. B., D. Foote, C. Forbes Perry, and G. D. Lindsay. 2003. Efficacy of aerial broadcast application of baits containing 0.005% diphacinone in reducing rat populations in Hawaiian forests. Unpublished report QA-2. U. S. Geological Survey, Pacific Island Ecosystems Research Center, Hawaii 191 pp.
- Stemmerman, L., and T. Ihsle. 1993. Replacement of *Metrosideros polymorpha*, `ohi`a, in Hawaiian dry forest succession. *Biotropica* **25**:36-45.
- Sugihara, R. T. 1997. Abundance and diets of rats in two native Hawaiian forests. *Pacific Science* **51**:189-198.
- Tamarin, T. H., and S. R. Malecha. 1971. The population biology of Hawaiian rodents: Demographic parameters. *Ecology* **52**:383-394.
- Timm, R. M. 1994a. House mice. Pages 31-46 in S. E. Hygnstrom, R. M. Timm, and G. E. Larson, editors. *Prevention and Control of Wildlife Damage*. University of Nebraska, Lincoln.
- Timm, R. M. 1994b. Norway rats. Pages 105-120 in S. E. Hygnstrom, R. M. Timm, and G. E. Larson, editors. *Prevention and Control of Wildlife Damage*. University of Nebraska, Lincoln.
- Tobin, M. E. 1994. Polynesian rats. Pages 121-124 in S. E. Hygnstrom, R. M. Timm, and G. E. Larson, editors. *Prevention and Control of Wildlife Damage*. University of Nebraska, Lincoln.

- Tobin, M. E., A. E. Koehler, and R. T. Sugihara. 1994. Seasonal patterns of fecundity and diet of roof rats in a Hawaiian macadamia orchard. *Wildlife Research* **21**:519-526.
- Tomich, P. Q. 1968. Coat color in wild populations of the roof rat in Hawaii. *Journal of Mammology* **49**:74-82.
- Tomich, P. Q. 1969. Mammals in Hawaii; a synopsis and notational bibliography. Bishop Museum Press, Honolulu.
- 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, editors. *Island Ecosystems*. University of Hawaii Press, Honolulu.
- Tomich, P. Q. 1986. *Mammals in Hawaii*. 2nd edition. Bishop Museum Press, Honolulu.
- Towns, D. R., I. A. E. Atkinson, C. H. Daugherty. 2006. Have the harmful effects of introduced rats on islands been exaggerated? *Biological Invasions* **8**:863-891
- Wirtz II, W. O. 1972. Population ecology of the Polynesian rat, *Rattus exulans*, on Kure Atoll, Hawaii. *Pacific Science* **26**:433-464.
- Yom-Tov, Y., S. Yom-Tov, and H. Moller. 1999. Competition, coexistence, and adaptation amongst rodent invaders to Pacific and New Zealand islands. *Journal of Biogeography* **26**:947-958.

**Table 1.** Trapping schedule for rodents at five sites in Hawai‘i Volcanoes National Park, Hawai‘i. Periods during which trapping was conducted are shaded grey.

<i>Year</i>	<i>Month</i>	<i>Season</i>	<i>MLS</i>	<i>KP</i>	<i>OLL</i>	<i>OLS</i>	<i>LL</i>
1986	Jul-Aug	Summer					
1988	Feb-Mar	Winter					
	Apr	Spring					
	Jun	Summer					
	July	Summer					
	Aug	Summer					
1989	Nov-Dec	Winter					
	Feb-Mar	Winter					
	Apr	Spring					
	May-Jun	Summer					
	Sep-Oct	Fall					
1990	Nov-Dec	Winter					
	Jan	Winter					
	May	Spring					

MLS = Mauna Loa Strip

KP = Kīpuka Puaulu

OLL = ‘Ōla‘a large tract

OLS = ‘Ōla‘a small tract

LL = Lowland (Nāulu and Kamoamoā)

**Table 2.** The mean (standard error) number of captures per100 trap nights per trapping session by species at five study sites in Hawai‘i Volcanoes National Park, Hawai‘i. Data were collected at Mauna Loa Strip (ML), Kīpuka Puaulu (KP), ‘Ōla‘a large tract (OLL), ‘Ōla‘a small tract (OLS), and in the National Park Lowlands (LL). Black and Polynesian rats were analyzed with ANOVA; Norway rats and mice were analyzed using a Kruskal-Wallis test. Values with the same superscript letter are not significantly different from one another according to Tukey’s HSD at  $\alpha = 0.05$ .

<i>Site</i>	<i>Black rats**</i>	<i>Polynesian rats***</i>	<i>Norway rats</i>	<i>Mice</i>
ML	2.10 (0.86) <sup>a</sup>	0.09 (0.08) <sup>a</sup>	0	4.16 (2.4)
KP	4.78 (0.93) <sup>b</sup>	3.33 (0.91) <sup>b</sup>	0	2.93 (0.89)
OLL	2.88 (0.5) <sup>a</sup>	0.39 (0.24) <sup>a</sup>	0.68 (0.47)	0
OLS	2.36 (0.5) <sup>a</sup>	1.26 (0.44) <sup>a,c</sup>	0.09 (0.08)	0
LL	2.12 (0.56) <sup>a</sup>	2.39 (0.39) <sup>b,c</sup>	0	0.99 (0.36)

\*\*  $P \leq 0.01$

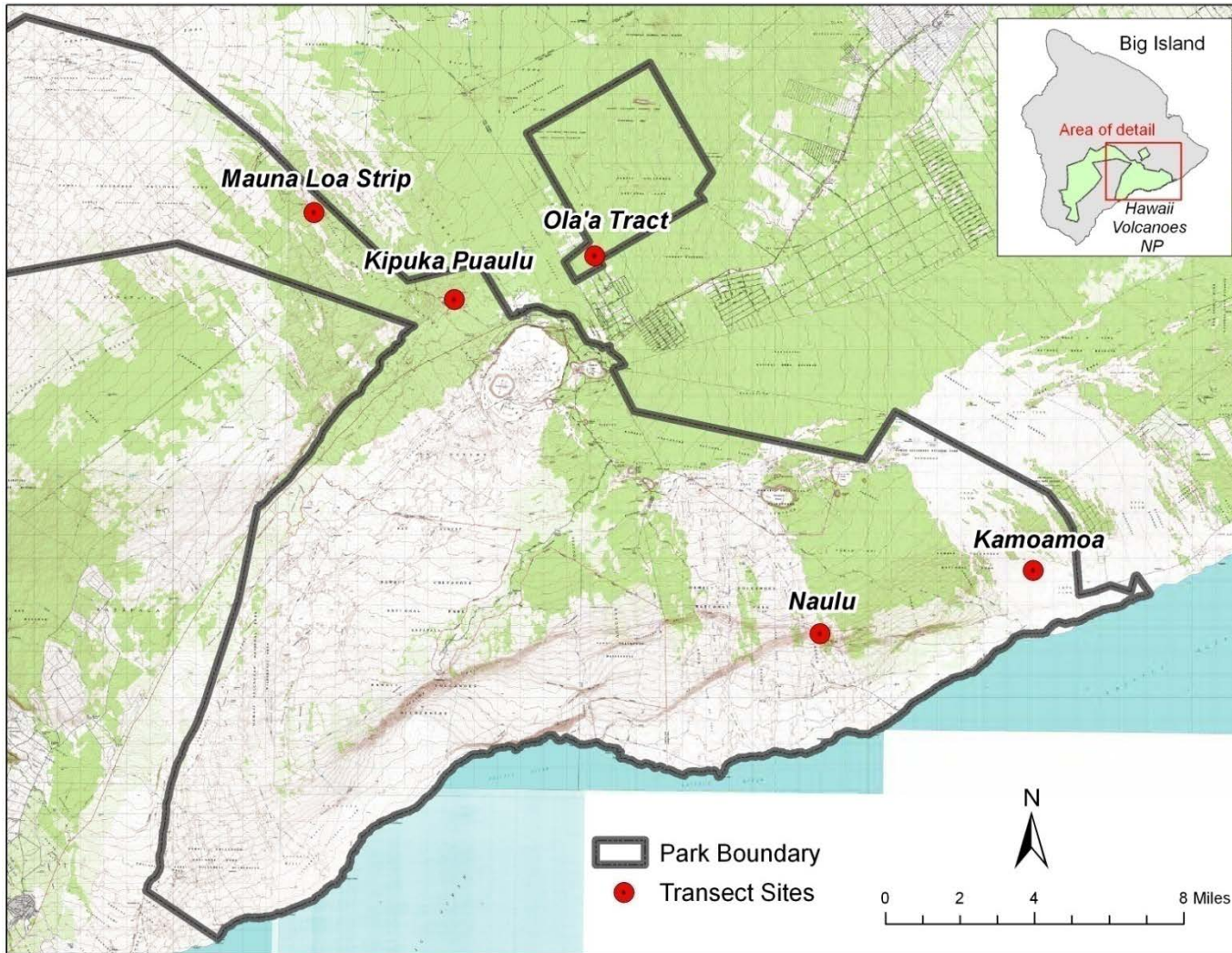
\*\*\*  $P \leq 0.001$

**Table 3.** The median weight at sexual maturity in grams and the number of reproductive individuals (n) used to obtain that weight for rodent species captured at each of five sites in Hawai‘i Volcanoes National Park, Hawai‘i. Data were collected at Mauna Loa Strip (ML), Kīpuka Puauulu (KP), ‘Ōla‘a large tract (OLL), ‘Ōla‘a small tract (OLS), and in the National Park Lowlands (LL).

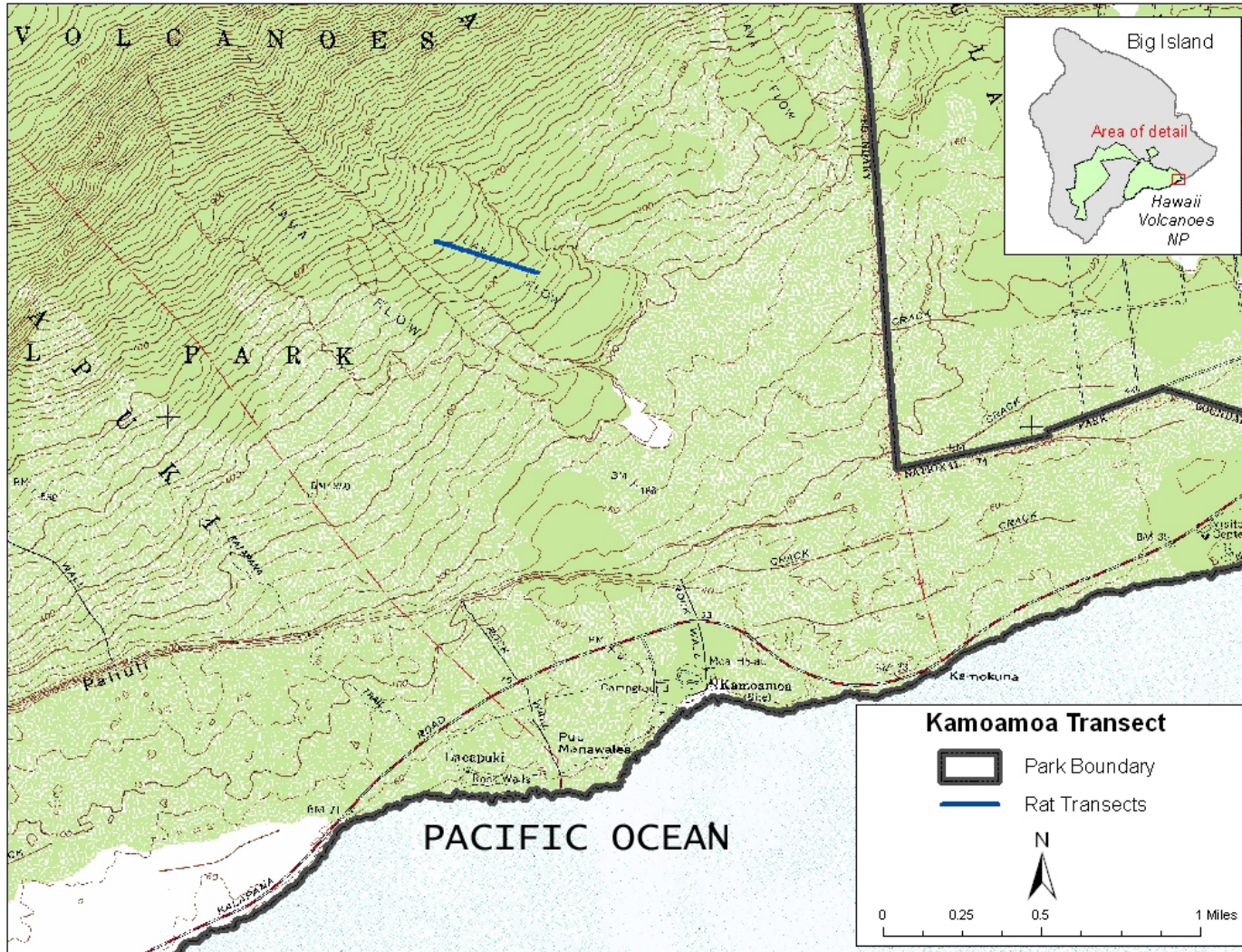
Site	Black rats		Polynesian rats		Norway rats		Mice	
	Male (n)	Female (n)	Male (n)	Female (n)	Male (n)	Female (n)	Male (n)	Female (n)
ML	136.5 (90)	136.0 (43)	68 (6)	58 (1)	n/a	n/a	14.0 (144)	14.0 (66)
KP	168.0 (110)	158.5 (19)	70.0 (65)	67.0 (21)	n/a	n/a	12.0 (58)	15.5 (18)
OLL	165.0 (80)	172.0 (19)	80.5 (16)	67.0 (1)	173.5 (12)	205.0 (5)	n/a	10.0 (1)
OLS	169.5 (138)	181.0 (42)	83.0 (81)	72.0 (41)	173.0 (7)	183.0 (2)	5.0 (1)	n/a
LL	140.0 (85)	128.0 (36)	66.0 (107)	65.0 (49)	n/a	n/a	14.0 (19)	14.0 (34)

**Table 4.** Distances (in meters) traveled by rodent species at the ‘Ōla‘a small tract (OLS) and Lowlands (LL) of Hawai‘i Volcanoes National Park, Hawai‘i. Distances are the minimum (i.e. shortest possible) distance between an assessment line and the point of capture of the individual. Mean distance (standard error) is the average minimum distance traveled by that species, shortest and longest are the range of minimum distances traveled by individuals of that species. Letters near the species name indicate significant groupings according to Tukey’s HSD at  $\alpha = 0.05$ .

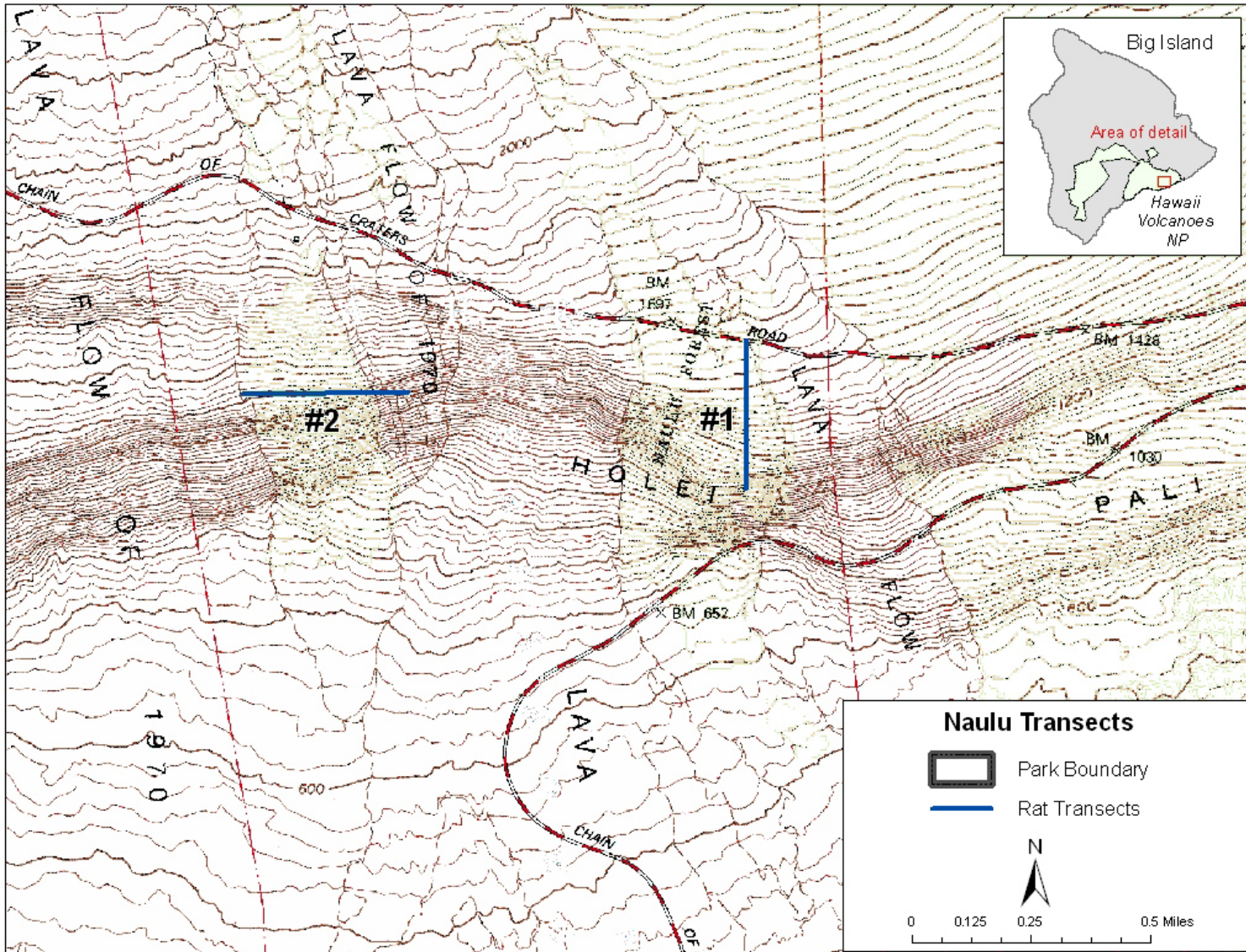
Species	Area	N	Mean	(SE)	Shortest	Longest
Black rats	OLS <sup>a</sup>	27	58.8	(5.4)	9.3	116.6
	LL	4	225.6	(103.7)	24.4	406.5
Norway rats	OLS <sup>b</sup>	4	153.9	(14.8)	118.9	179.5
Polynesian rats	OLS <sup>a</sup>	11	67.2	(11.4)	4.7	149.2
	LL	17	54.8	(17.4)	4.1	256.1



**Figure 1.** The location of the five study areas within Hawai'i Volcanoes National Park, Hawai'i. Four transects were located in the Mauna Loa Strip site, two at Kipuka Puauulu, four at the 'Ōla'a Forest (two each in the large and small tract units), two at Nāulu and one at Kamoamo. Together Nāulu and Kamoamo comprise the Lowland site.

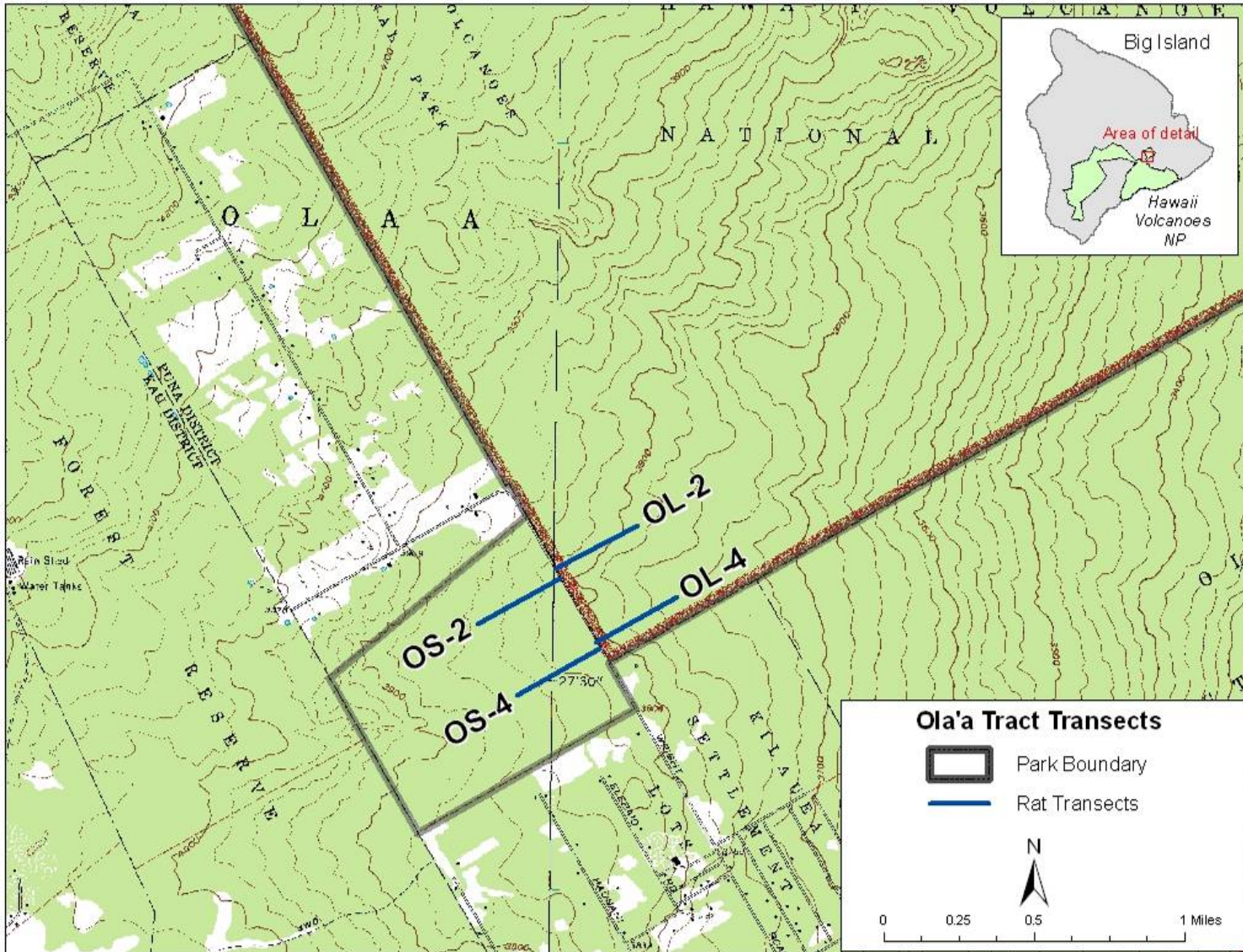


**Figure 2.** The location of the Kamoamo transect in the Lowlands, Hawai'i Volcanoes National Park, Hawai'i.

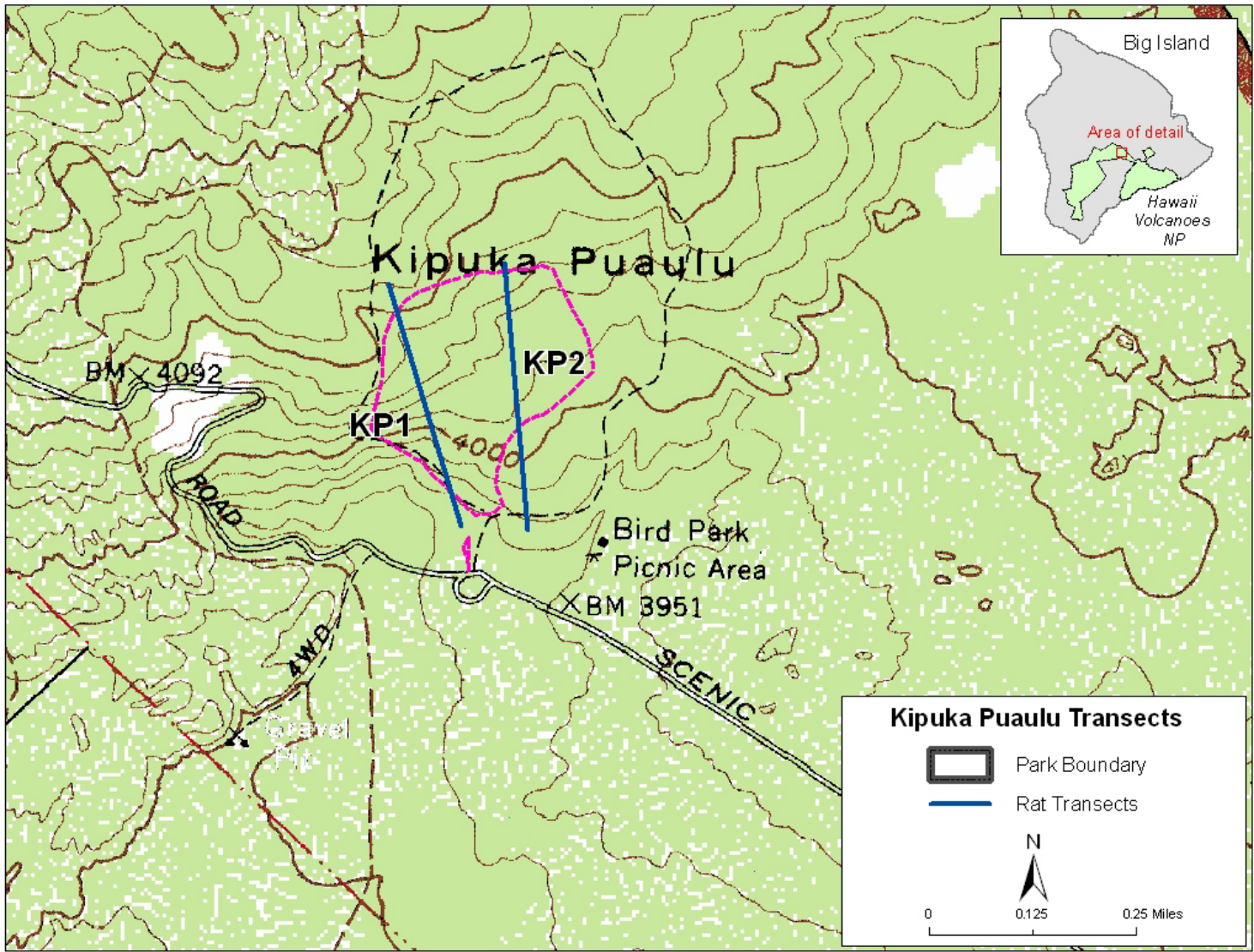


**Figure 3.** The location of the two Nāulu transects in the Lowlands, Hawai'i Volcanoes National Park, Hawai'i.

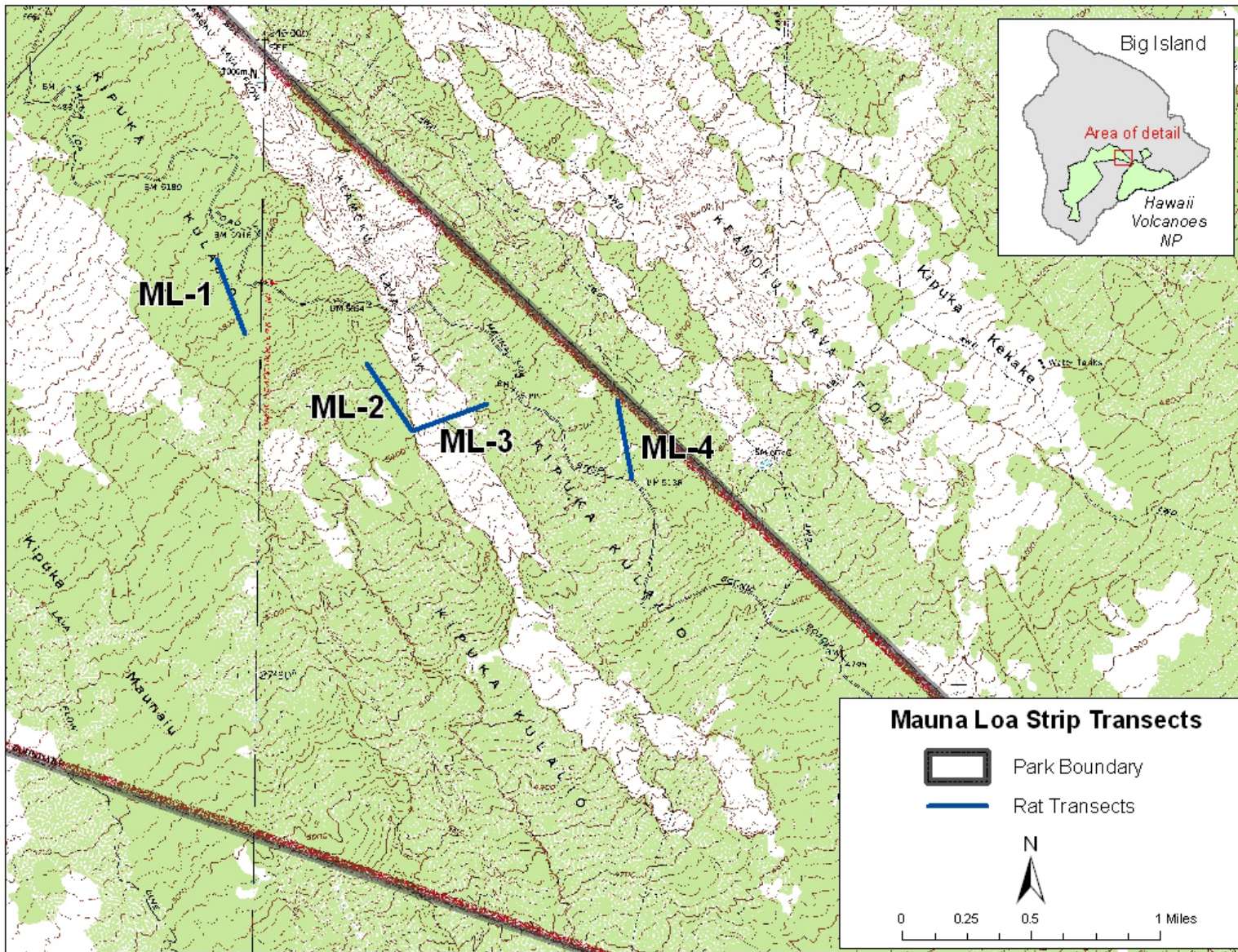




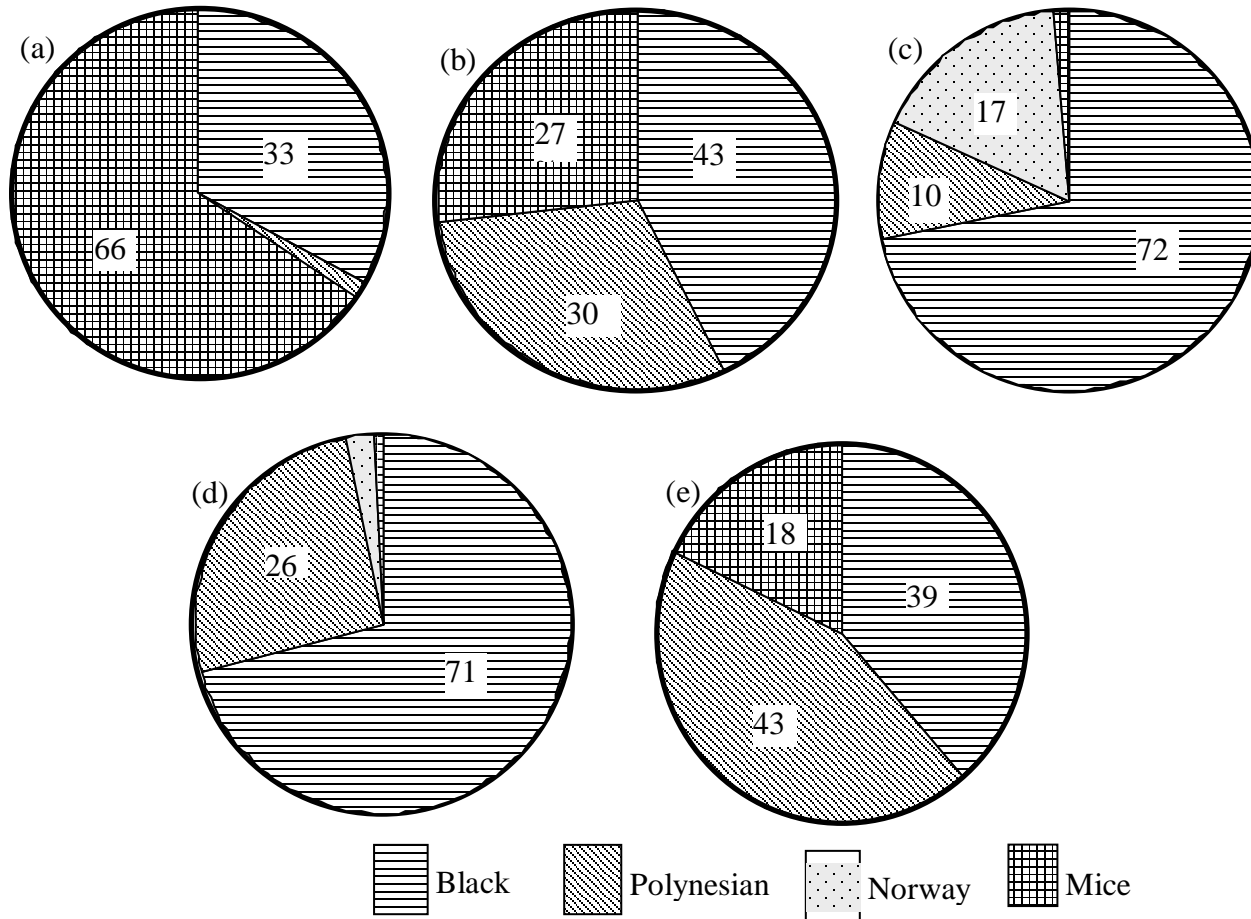
**Figure 4.** The location of the transects in the 'Ōla'a Large (OL-2, OL-4) and 'Ōla'a Small (OS-2, OS-4) Tract, Hawaii'i Volcanoes National Park, Hawaii'i.



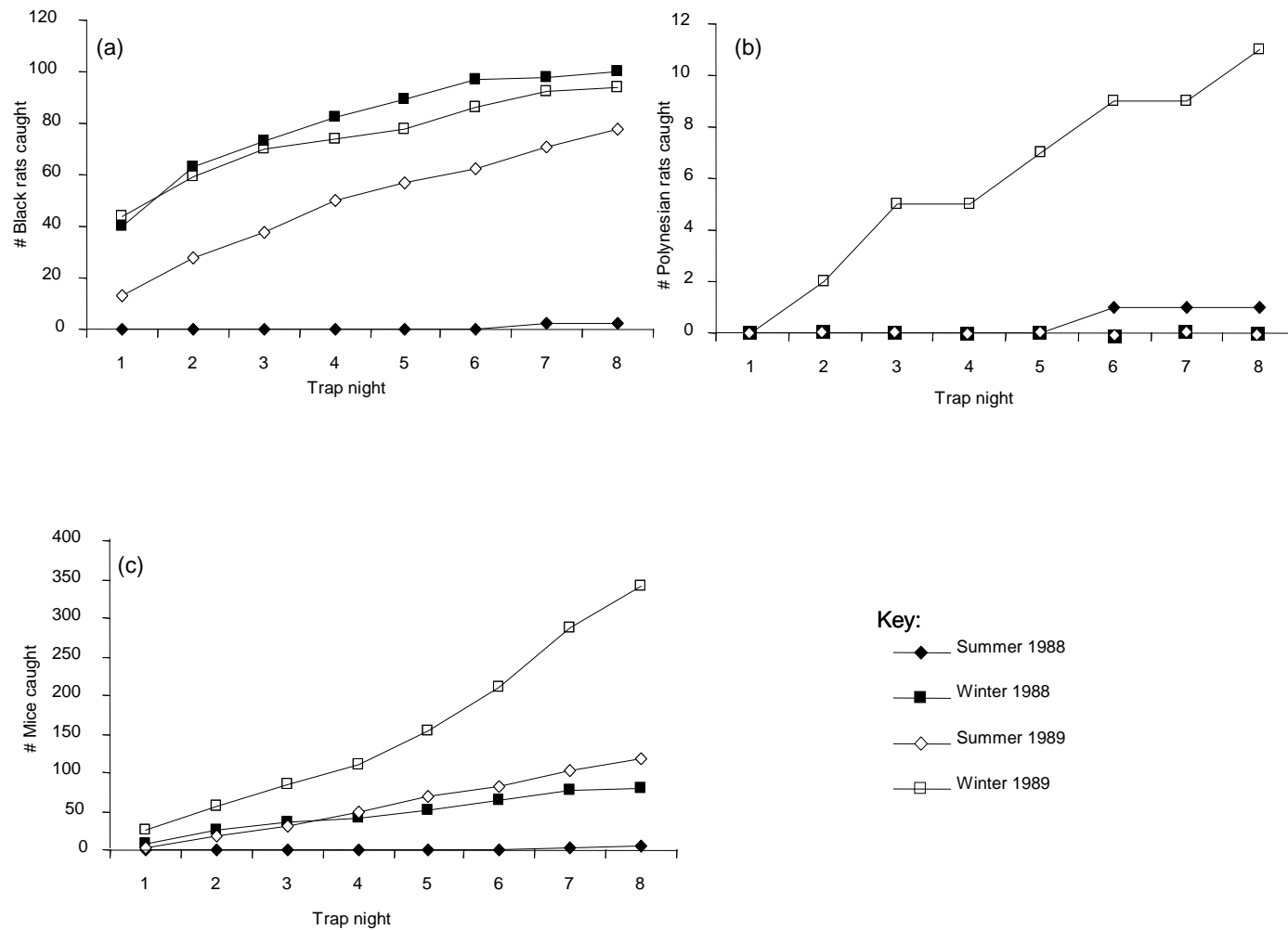
**Figure 5.** The location of the two transects at Kīpuka Puauū, Hawai‘i Volcanoes National Park, Hawai‘i. The Kīpuka Puauū trail (pink line) is shown for reference.



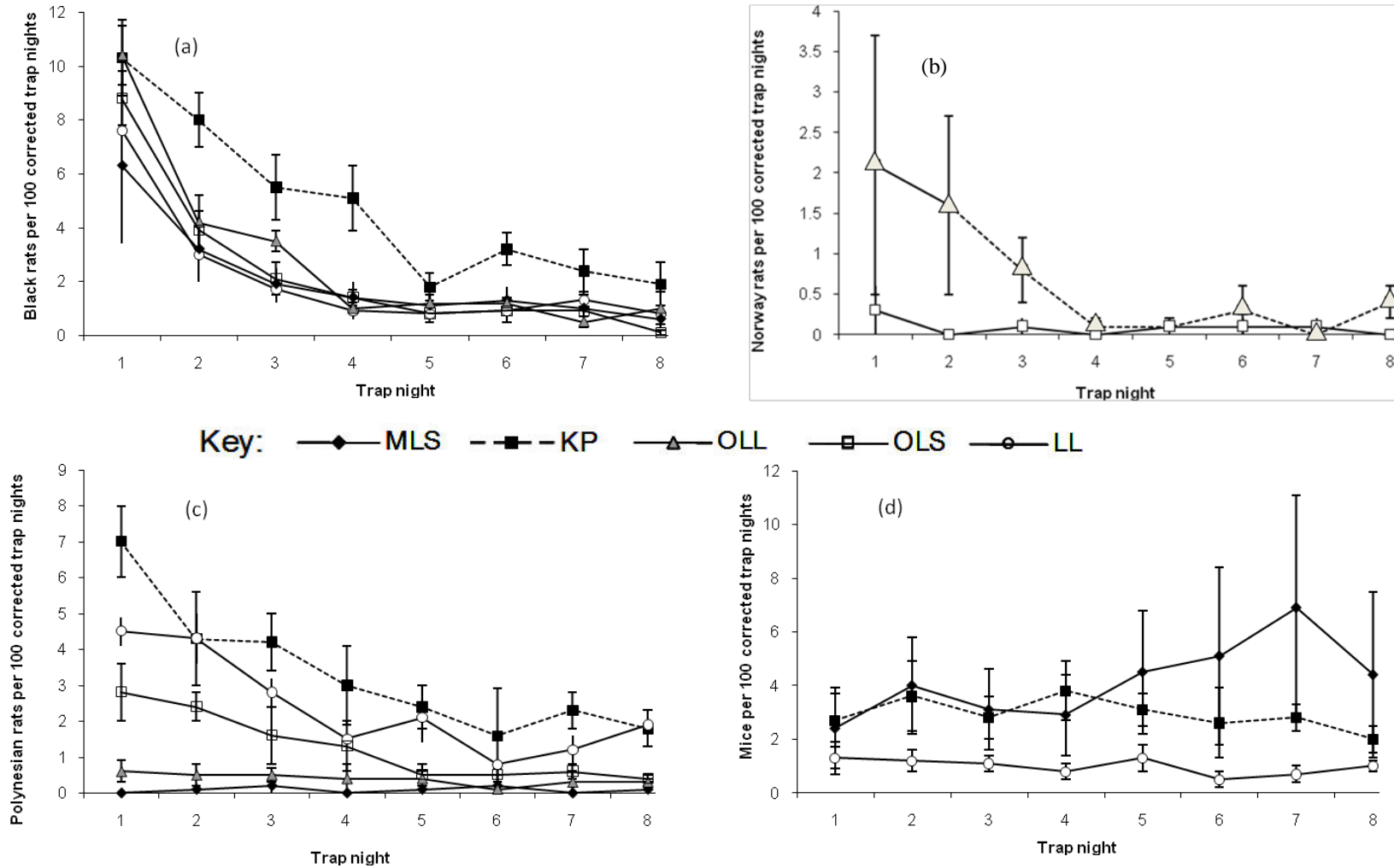
**Figure 6.** The location of the four transects at the Mauna Loa Strip site, Hawai'i Volcanoes National Park, Hawai'i.



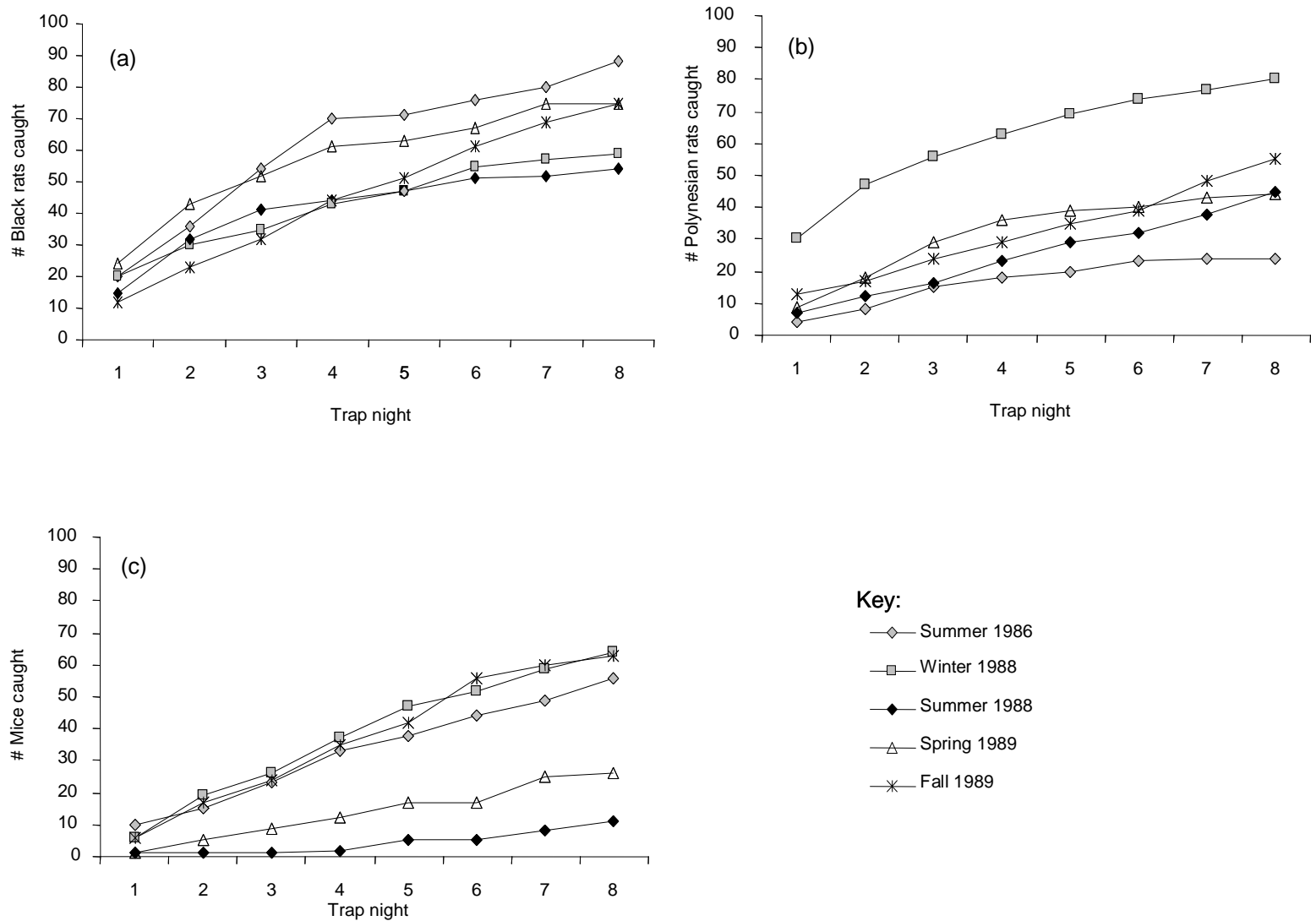
**Figure 7.** Rodent species composition (total individuals per trap night) at the five study sites: (a) Mauna Loa Strip, (b) Kīpuka Puauulu, (c) 'Ōla'a large tract, (d) 'Ōla'a small tract, and (e) Lowlands. The percent of the overall rodent community is noted on the figures for species which comprised ten-percent or more of the total capture.



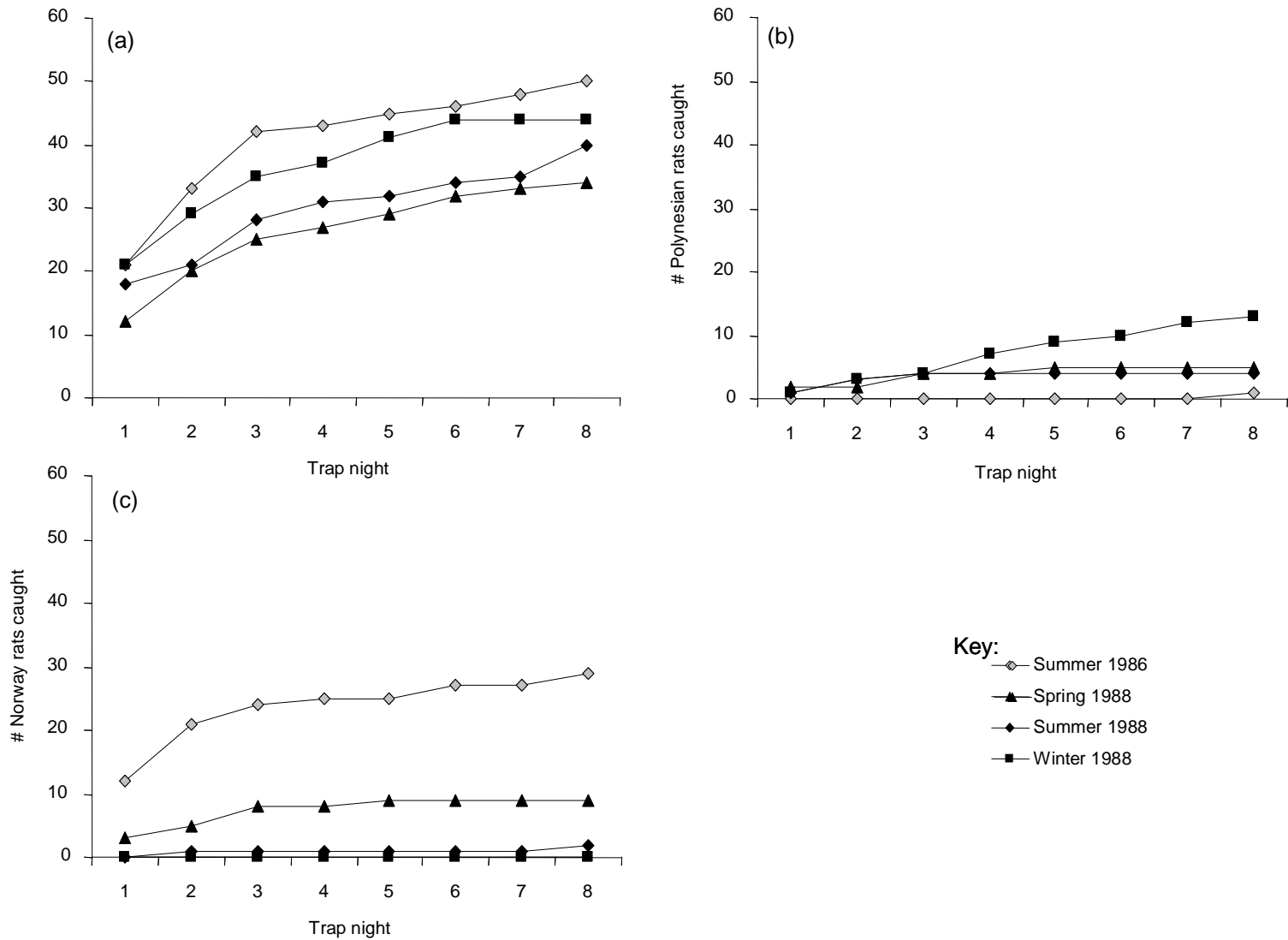
**Figure 8.** Capture rate (accumulation curves) for rodents trapped in eight-day periods over four trapping sessions at the Mauna Loa Strip, Hawai'i Volcanoes National Park, Hawai'i: (a) black rats, (b) Polynesian rats, (c) mice; note that the y-scale is not consistent across figures.



**Figure 9.** The mean number of rodents caught per 100 corrected trap nights over the eight trap nights at the five study sites: (a) black rats, (b) Norway rats, (c) Polynesian rats, and (d) mice. MLS = Mauna Loa Strip, KP = Kīpuka Puau, OLL = ‘Ōla’a large tract, OLS = ‘Ōla’a small tract, LL = Lowlands. Error bars represent standard error of the mean. Note that y-axes have different scales.

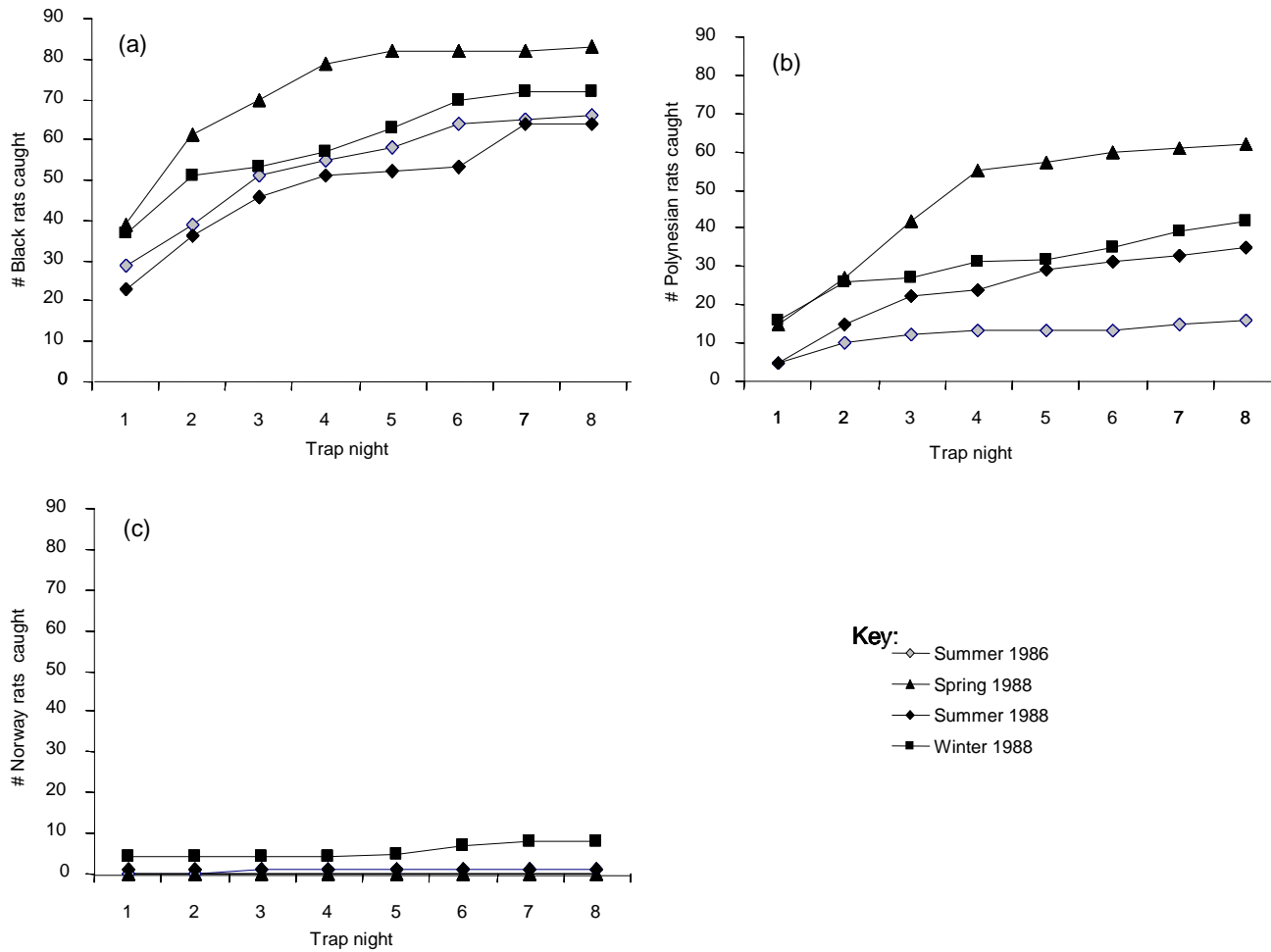


**Figure 10.** Capture rate (accumulation curves) for rodents trapped in eight-day periods over five trapping sessions at Kīpuka Puau, Hawai‘i Volcanoes National Park, Hawai‘i: (a) black rats, (b) Polynesian rats, (c) mice.

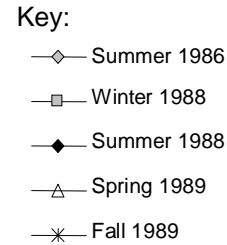
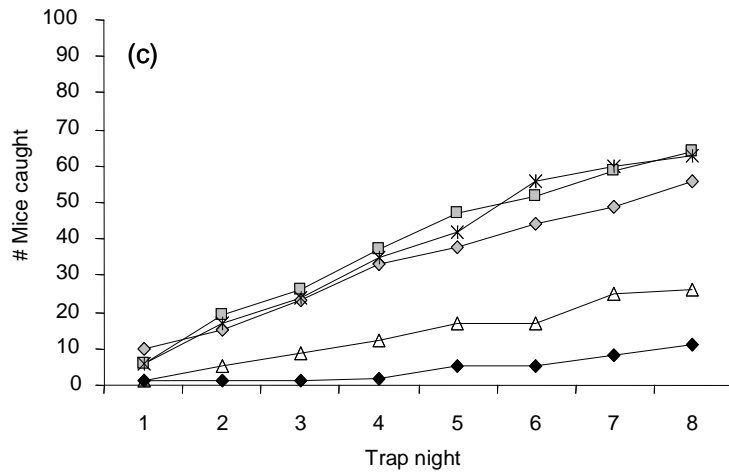
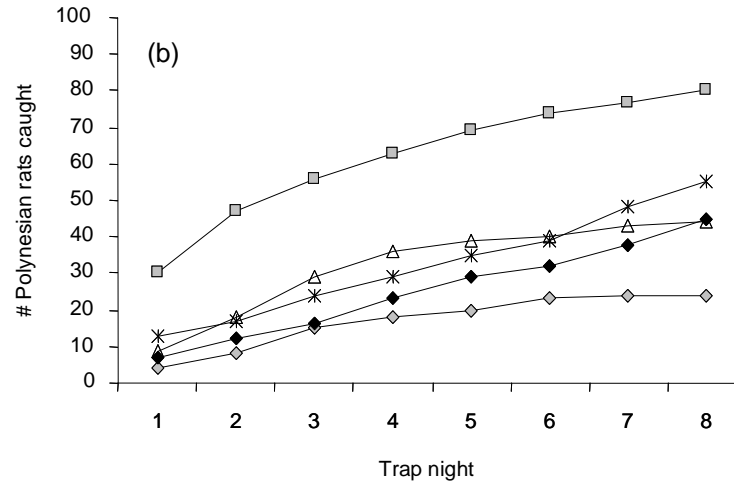
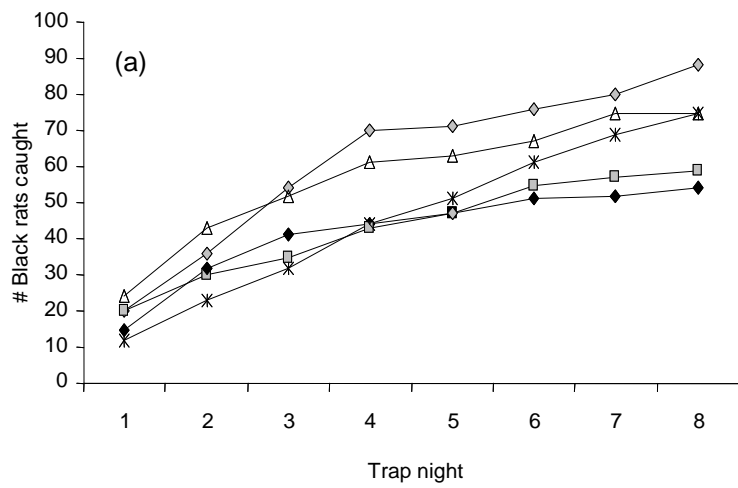


**Figure 11.** Capture rate (accumulation curves) for rodents trapped in eight-day periods over four trapping sessions at 'Ōla'a Forest large tract, Hawai'i Volcanoes National Park, Hawai'i: (a) black rats, (b) Polynesian rats, (c) Norway rats.

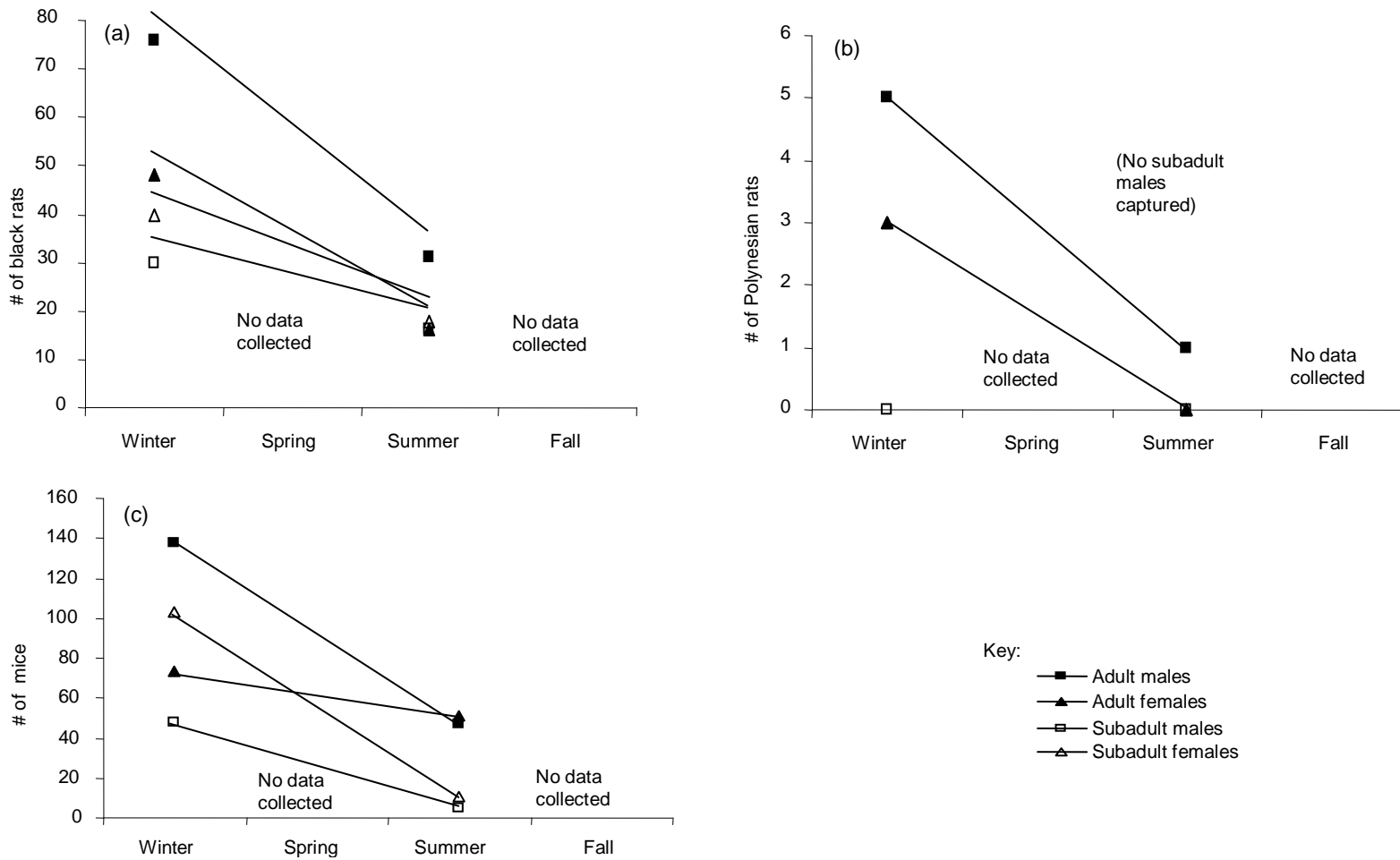




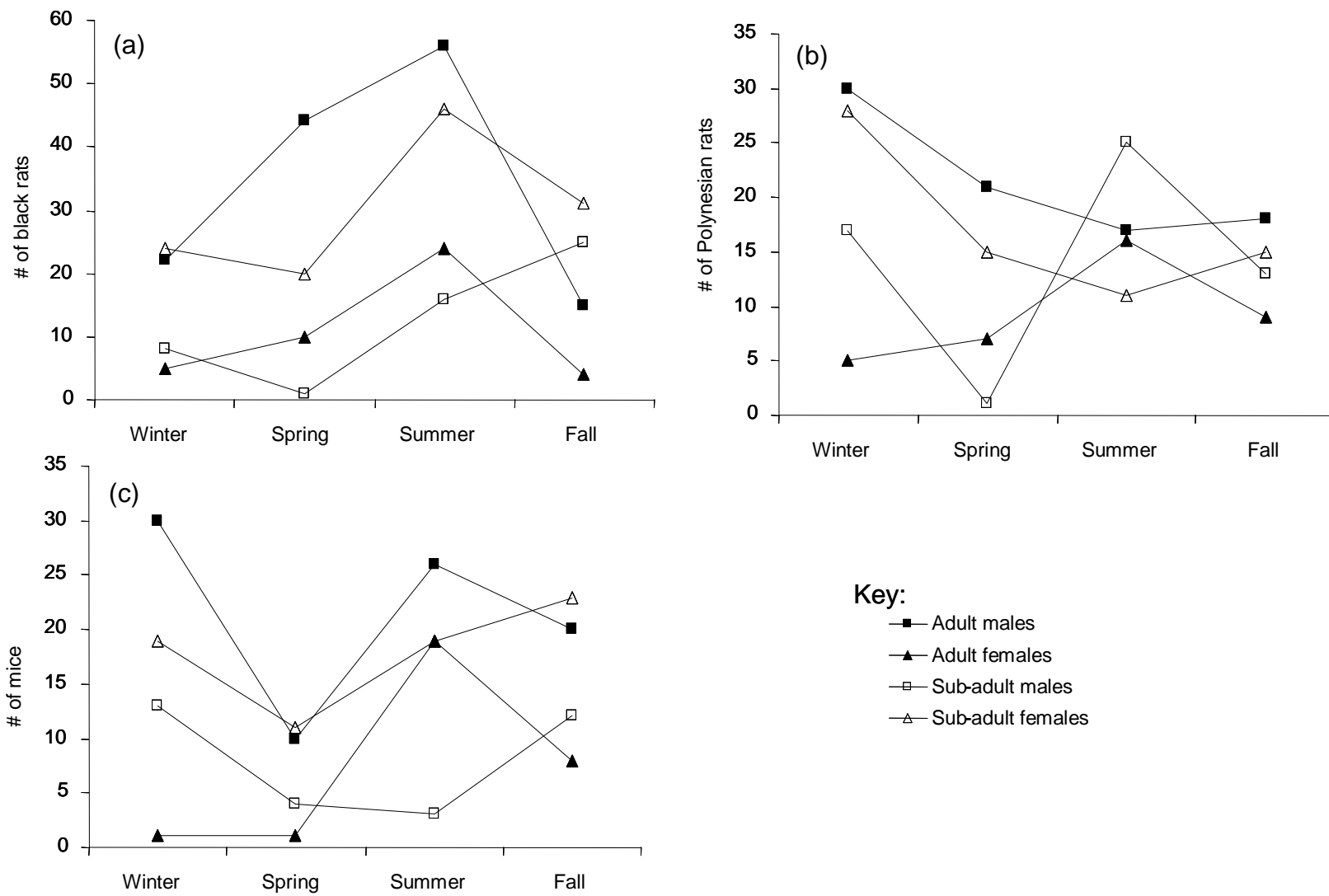
**Figure 12.** Capture rates (accumulation curves) for three species of rodent trapped in eight-day periods over four trapping sessions at ‘Ōla‘a Forest small tract, Hawai‘i Volcanoes National Park, Hawai‘i: (a) black rats, (b) Polynesian rats, (c) Norway rats.



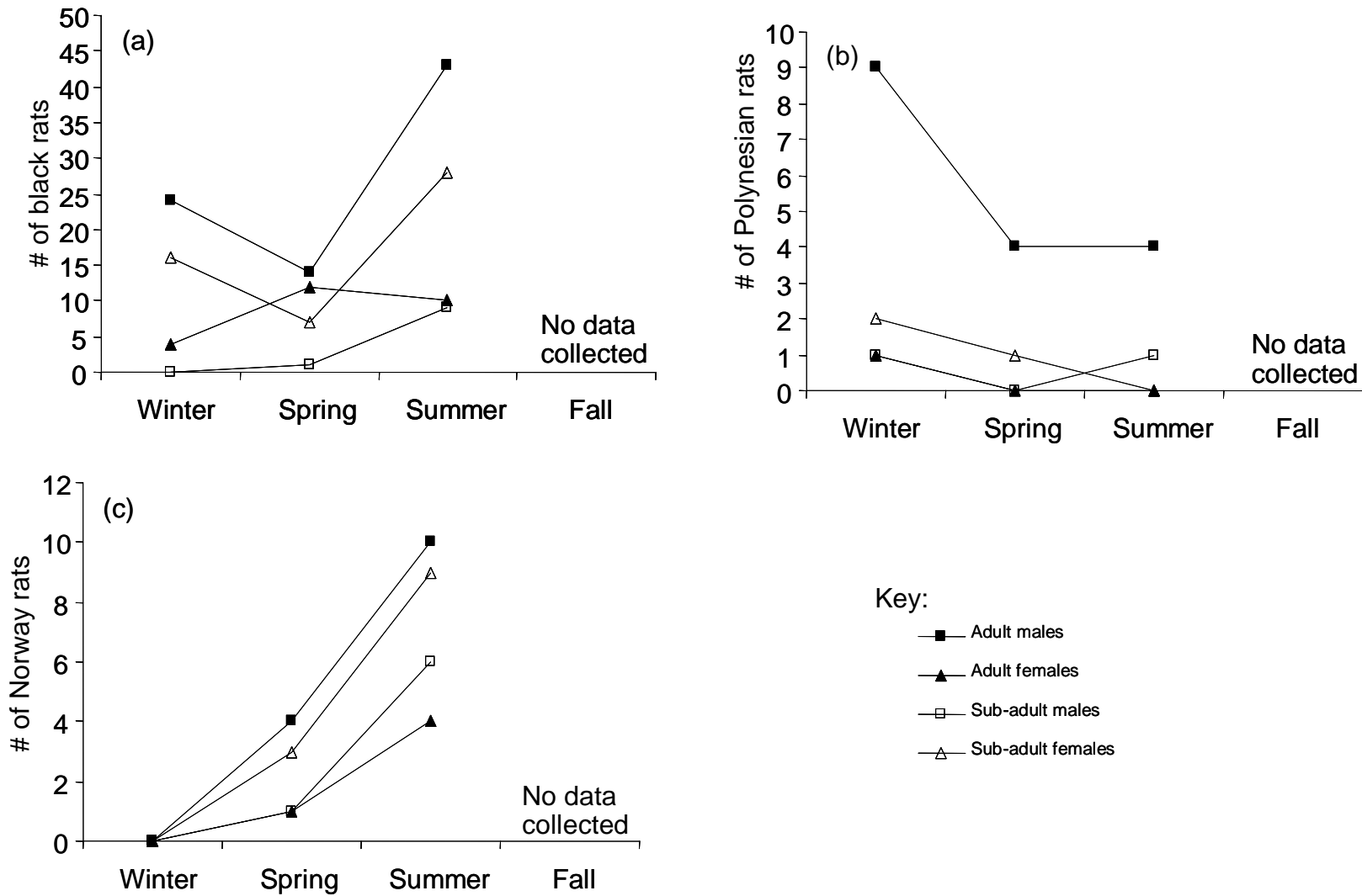
**Figure 13.** Capture rate (accumulation curves) for rodents trapped in eight-day periods over four trapping sessions in the Lowlands of Hawai'i Volcanoes National Park, Hawai'i: (a) black rats, (b) Polynesian rats, (c) mice.



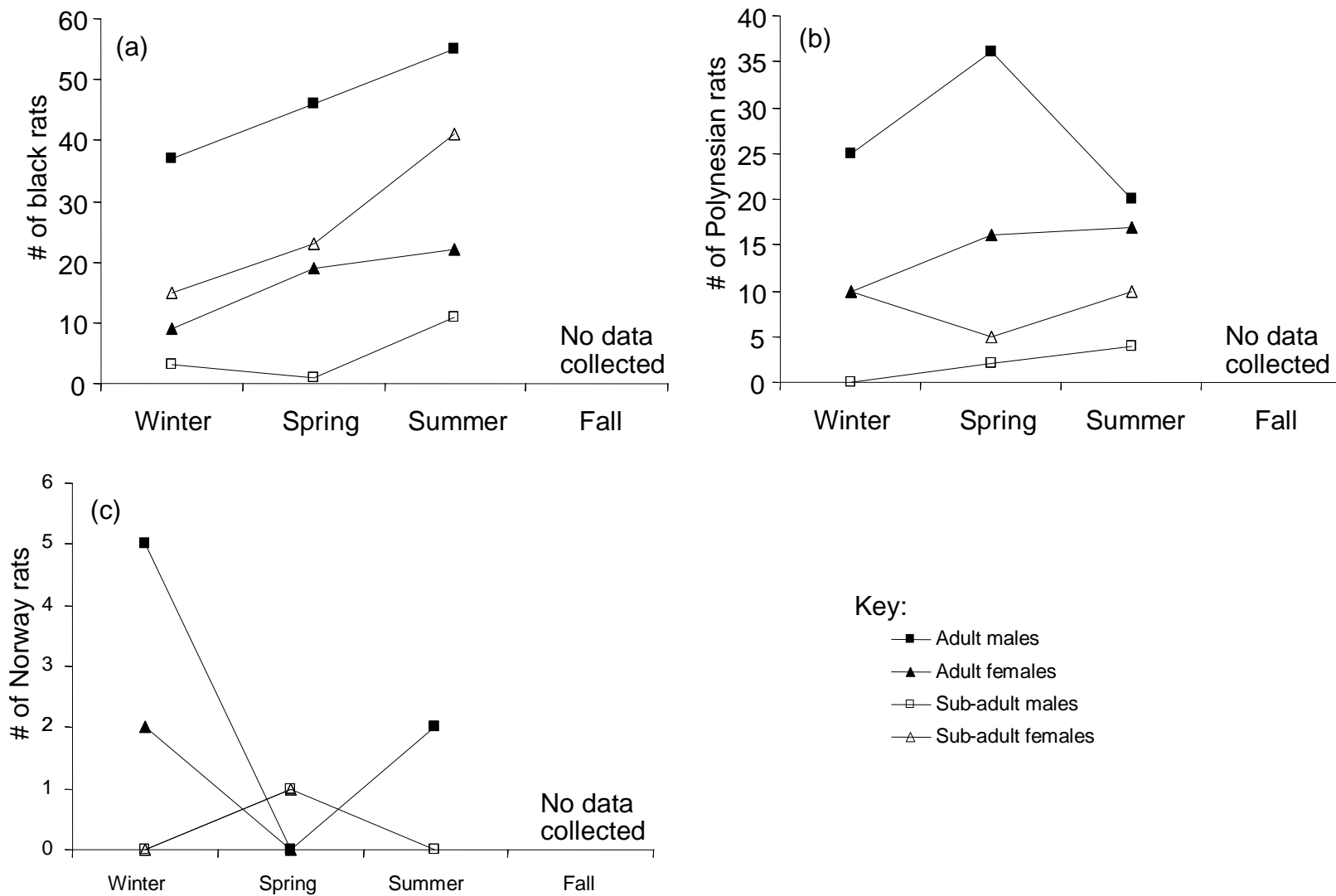
**Figure 14.** Age structure for rodent captures at the Mauna Loa Strip, Hawai'i Volcanoes National Park, Hawai'i: (a) black rats, (b) Polynesian rats, (c) mice.



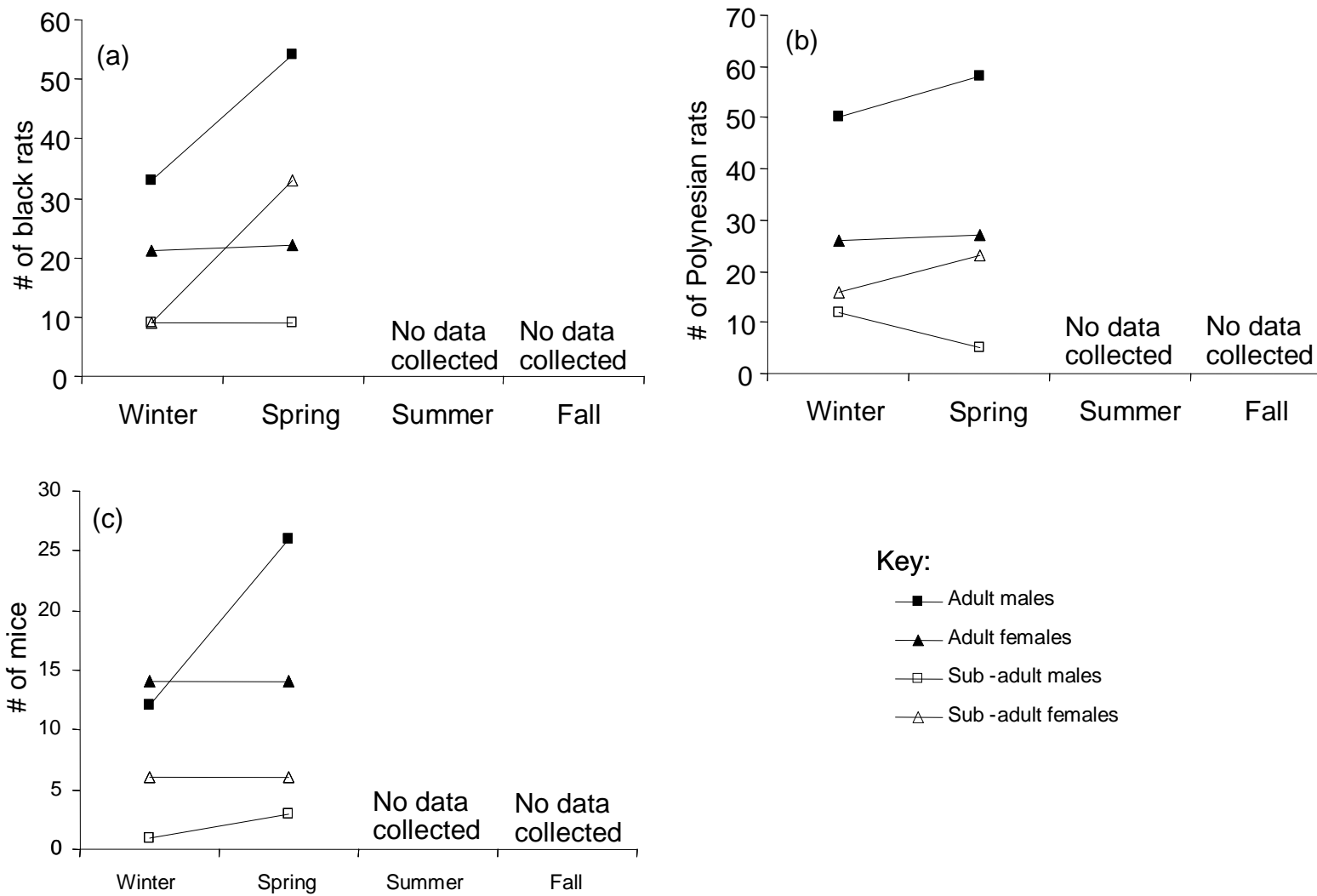
**Figure 15.** Age structure for rodent captures at Kīpuka Puauulu, Hawai‘i Volcanoes National Park, Hawai‘i: (a) black rats, (b) Polynesian rats, (c) mice.



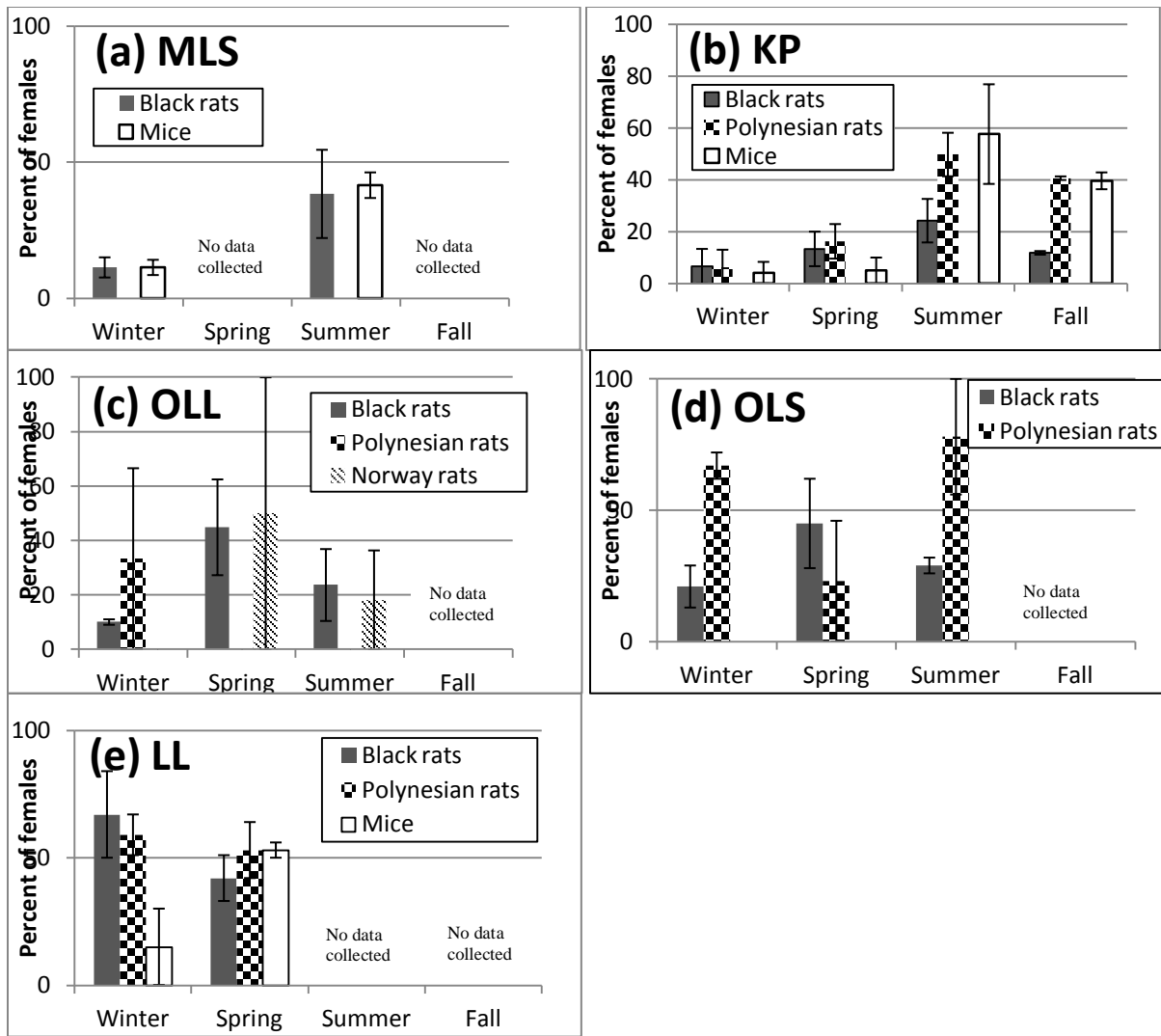
**Figure 16.** Age structure for rodent capture at the ‘Ōla‘a Forest large tract, Hawai‘i Volcanoes National Park, Hawai‘i: (a) black rats, (b) Polynesian rats, (c) Norway rats. Solid symbols are adult captures, hollow symbols are juvenile (see key).



**Figure 17.** Age structure for rodent capture at the ‘Ōla‘a Forest small tract, Hawai‘i Volcanoes National Park, Hawai‘i: (a) black rats, (b) Polynesian rats, (c) Norway rats. Solid symbols are adult captures, hollow symbols are juvenile (see key).

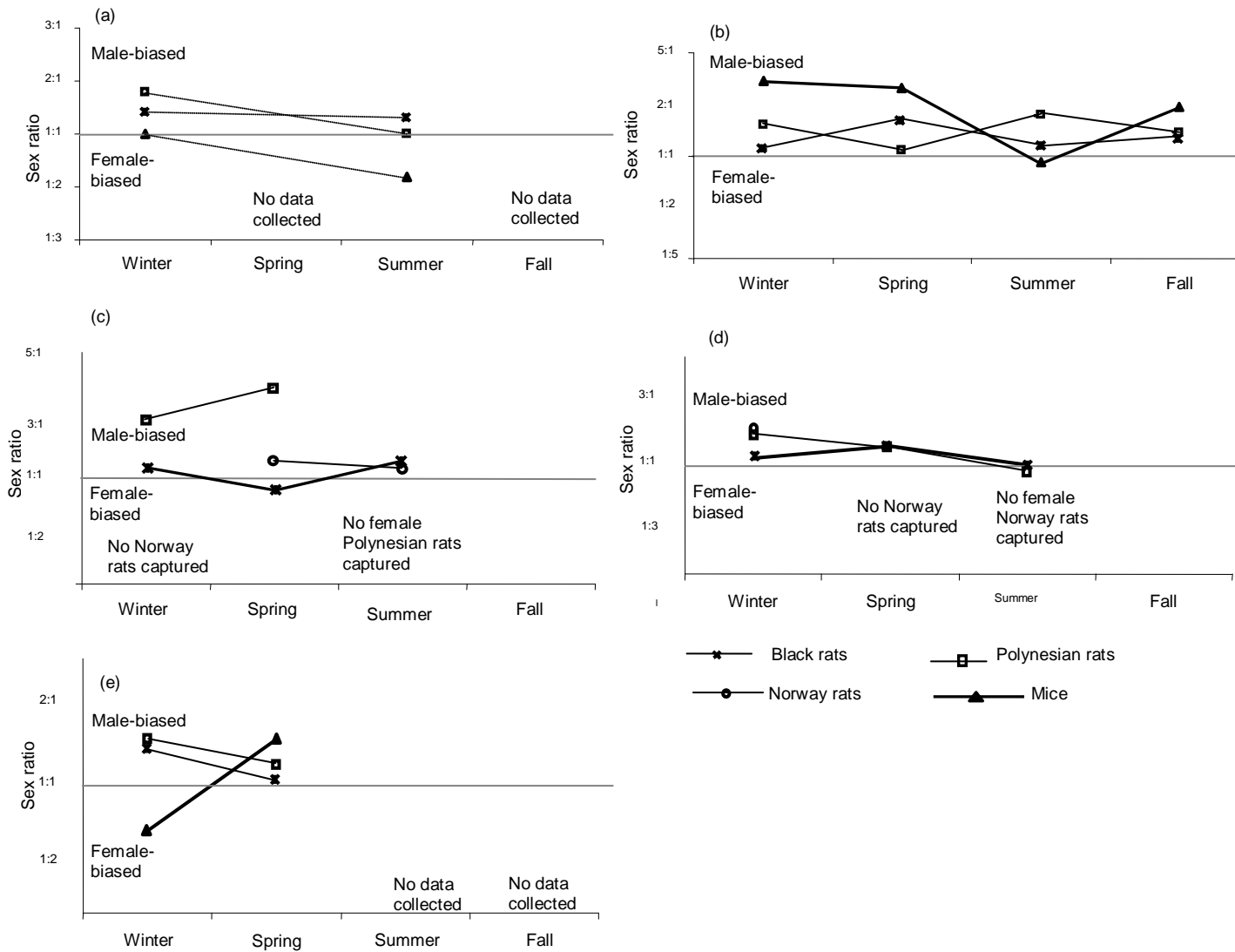


**Figure 18.** Age structure for rodent captures in the Lowlands of Hawai‘i Volcanoes National Park, Hawai‘i: (a) black rats, (b) Polynesian rats, (c) mice. Solid symbols are adult captures, hollow symbols are juvenile (see key).

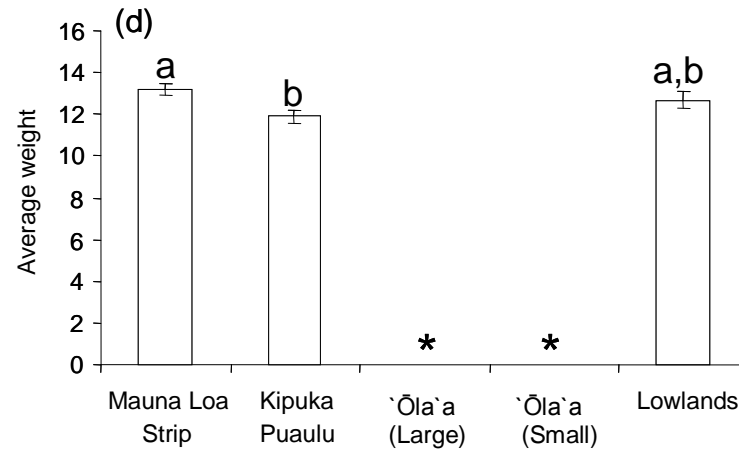
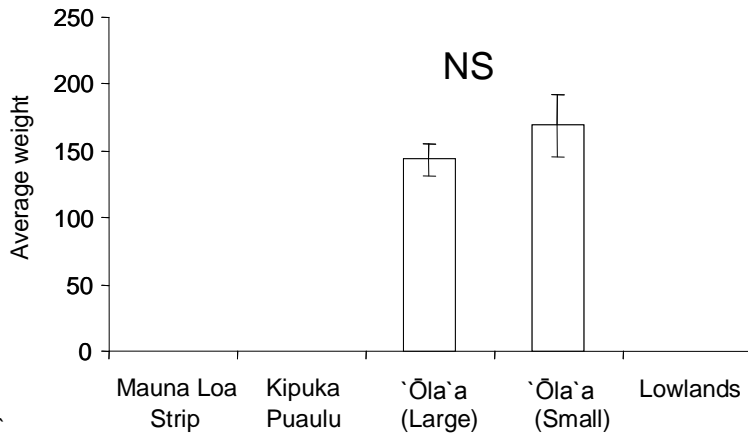
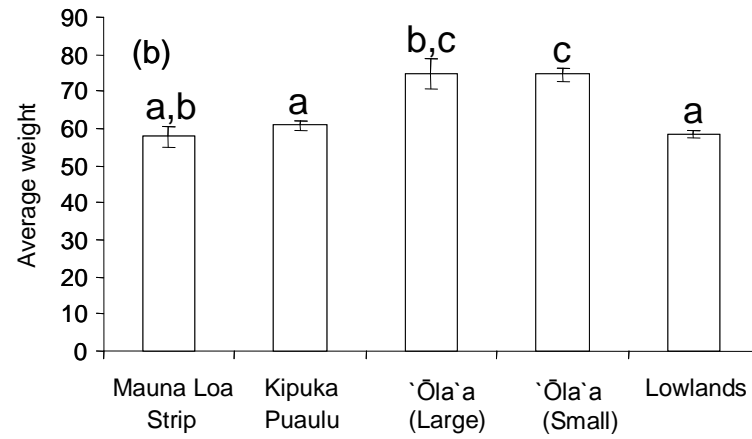
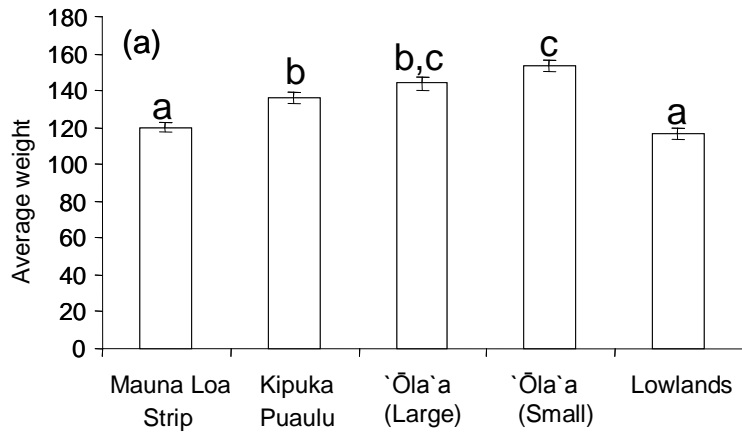


**Figure 19.** The mean percentage of reproductive female rodents across seasons at the five study sites in Hawai‘i Volcanoes National Park, Hawai‘i: (a) Mauna Loa Strip, (b) Kīpuka Puauulu, (c) ‘Ōla‘a Forest large tract, (d) ‘Ōla‘a Forest small tract, and (e) Lowlands. Error bars represent the standard error of the mean.



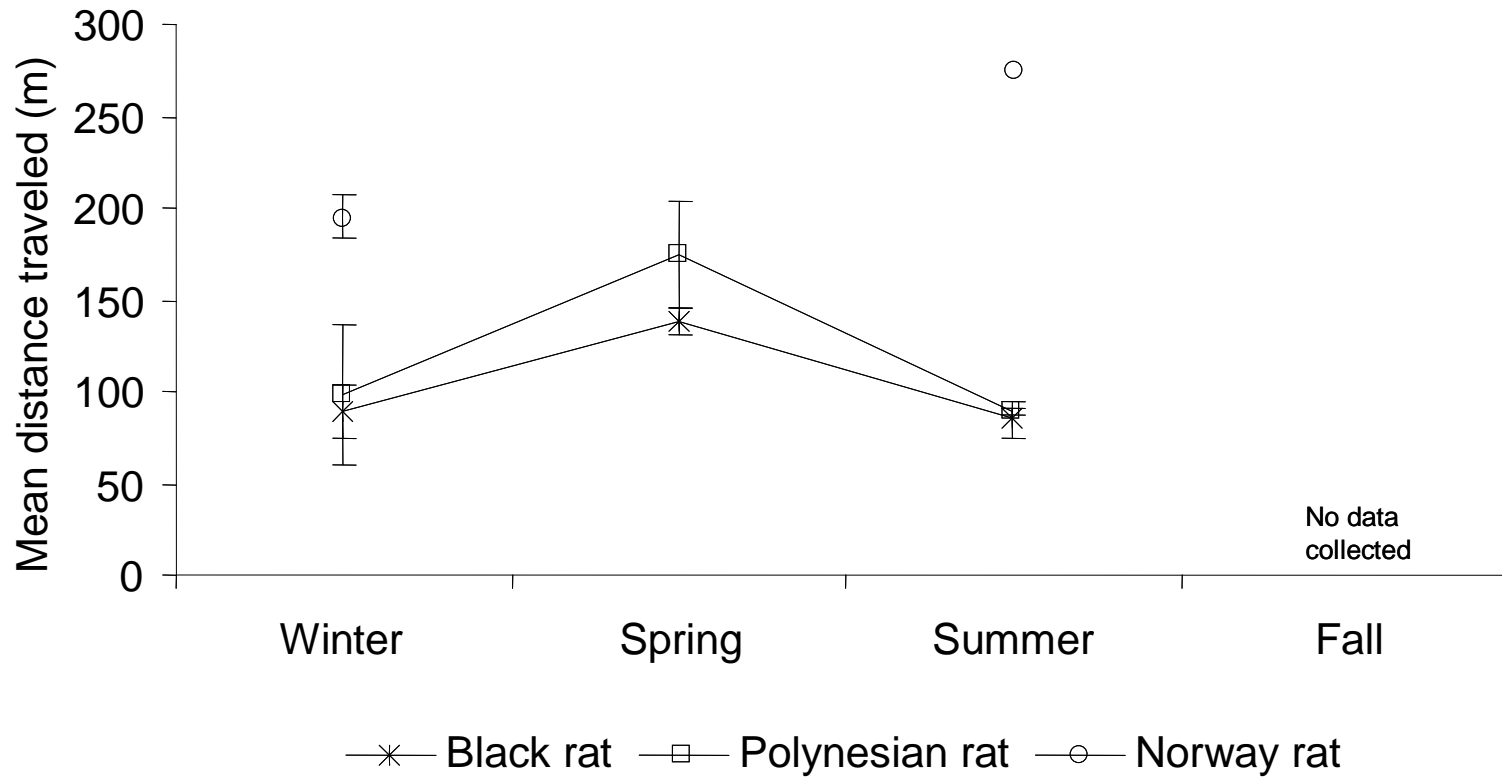


**Figure 20.** Seasonal sex ratio for the four rodent species found at the five Hawai'i Volcanoes National Park study sites, Hawai'i: (a) Mauna Loa Strip, (b) Kīpuka Puaulu, (c) 'Ōla'a Forest large tract, (d) 'Ōla'a Forest small tract, and (e) Lowlands.

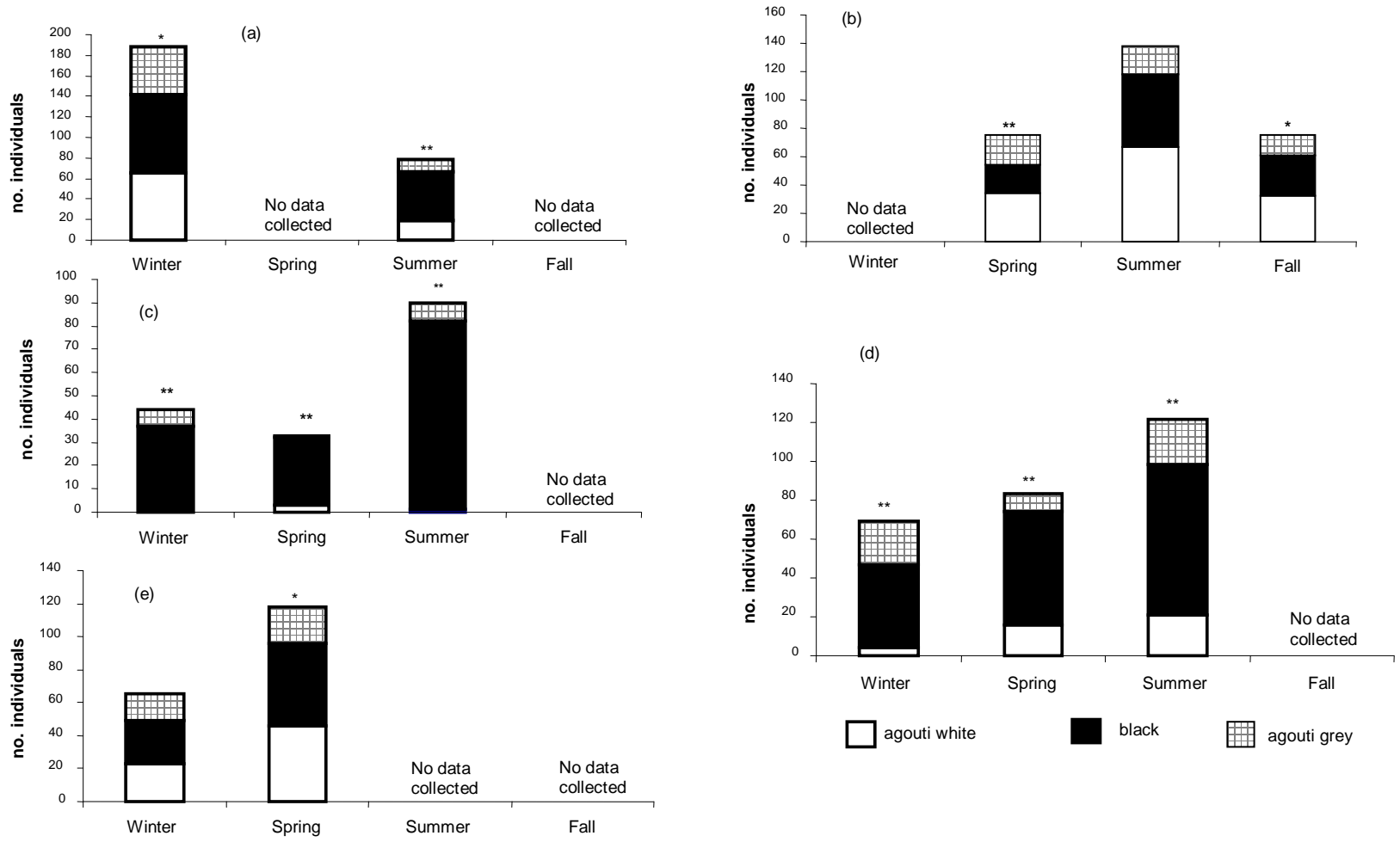


\* too few captures to accurately analyze accurately.

**Figure 21.** Mean weight of the four rodent species found at the five study sites in Hawai'i Volcanoes National Park, Hawai'i. (a) black rats, (b) Polynesian rats, (c) Norway rats, and (d) mice. Error bars represent standard error of the mean. Letters above the bars indicate significant groupings according to Tukey's HSD at  $\alpha = 0.05$ .



**Figure 22.** Distances traveled by the three most common species of rodents in the Ōla‘a Forest small tract, Hawai‘i Volcanoes National Park, Hawai‘i, during the three seasons of the study. Rodents captured include black rats, Polynesian rats, and Norway rats. Error bars represent the standard error of the mean.



**Figure 23.** Seasonal change in pelage color for black rats at the five Hawai'i Volcanoes National Park study sites, Hawai'i: (a) Mauna Loa Strip, (b) Kīpuka Puauu, (c) 'Ōla'a Forest large tract, (d) 'Ōla'a Forest small tract, and (e) Lowlands. Asterisks indicate ratios that deviate significantly from a 1:1:1 ratio (Chi-square). \*  $P \leq 0.05$ , \*\*  $P \leq 0.001$ .