

**Seasonal activity and movements of *Rattus rattus*
(Rodentia, Muridae)
in a Hawaiian macadamia orchard**

by M.E. TOBIN¹, R.T. SUGIHARA¹, A.E. KOEHLER¹ and G.R. UEUNTEN²

¹ U.S. Department of Agriculture, Denver Wildlife Research Center,
P.O. Box 10880, Hilo, HI 96721 U.S.A.

M.E. Tobin : Current address : U.S. Department of Agriculture, Denver Wildlife
Research Center, P.O. Drawer 6099, Mississippi State, MS 39762 U.S.A.

² Mauna Loa Macadamia Nut Corporation, HC/01 Box 3, Hilo, HI 96720 U.S.A.

Summary. – We determined activity and movements of *Rattus rattus* in a Hawaiian macadamia (*Macadamia integrifolia*) orchard from 3,006 radio locations of 54 individuals during 3 periods of the crop cycle. Most rats remained in burrows during the day, emerged 1-2 hours after sunset, ascended into the canopy, and returned to their burrows 1-2 hours before sunrise. Minimum convex polygon home ranges averaged 0.20 ha (SE = 0.02) and did not vary between sexes ($P = 0.17$) or among peak anthesis (flowering), midseason, and peak harvest ($P = 0.54$). Movements as measured by median distance from center of activity averaged 15.4 m (range = 5.6 – 35.7 m) and also did not vary between sexes ($P = 0.66$) or among periods of the crop cycle ($P = 0.10$). Only 2 of 51 rats initially captured in the orchard ventured outside the study block. Rats selectively ($P = 0.009$) utilized variety 660 compared to variety 508 when the former variety had an abundance of mature or nearly mature nuts. Managers should concentrate damage control efforts in the orchard rather than adjacent windbreaks and waste areas, should place rodenticide baits directly in burrows or trees at ≥ 5 locations/ha, and may be able to reduce rodenticide use by selectively baiting in tree varieties that have mature nuts.

Résumé. – Nous avons déterminé l'activité et le déplacement de *Rattus rattus* dans un verger de macadamia (*Macadamia integrifolia*) à partir de 3 006 points de radio-pistage, de 54 individus, pendant une période de trois cycles de récolte. La plupart des rats restaient dans des terriers pendant le jour, sortaient 1-2 heures après le coucher de soleil, montaient dans le feuillage, et retournaient dans leurs terriers 1-2 heures avant l'aube. Le domaine vital calculé par la méthode du polygone convexe minimal était, en moyenne, de 0,20 ha (SE = 0,18) et ne variait pas entre les sexes ($P = 0,17$) ou pendant les floraisons maximales, la moyenne saison, et la pleine récolte ($P = 0,54$). Les déplacements mesurés par la distance médiane au centre d'activité étaient, en moyenne, de 15,4 m (champ = 5,6 – 35,7 m) et ne variaient pas entre les sexes ($P = 0,66$) ou pendant les périodes de cycle de récolte ($P = 0,10$). Seulement 2 des 51 rats capturés initialement dans le verger se sont aventurés en dehors du champ d'étude. Sélectivement, des rats ($P = 0,009$) profitèrent de la variété 660 comparée à la variété 508 quand la première avait une abondance de noix mûres ou presque mûres. Les administrateurs devraient concentrer leurs efforts, pour contrôler les dégâts, dans les vergers, plutôt que dans les andains adjacents et dans les terres autour, ils devraient placer les raticides directement dans les terriers ou dans les arbres à raison de 5 plaquettes par hectare, et ils pourraient peut-être réduire l'utilisation du raticide en piégeant d'une manière sélective les variétés d'arbre qui ont des noix mûres.

INTRODUCTION

Black rats damage about 5 % of the developing macadamia nut crop in Hawaii (Fellows 1982, Tobin *et al.* 1993), resulting in estimated farm-value losses of about \$1.7 million during the 1991-92 crop season (Hawaii Agricultural Statistics Service 1992). These pests climb into the canopy of macadamia trees and feed on developing nuts from the time the kernels are small, unprotected fruits to when they are fully developed and surrounded by hard shells and fibrous husks. Damaged nuts either are detached by rats during feeding or abscise prematurely and drop to the ground.

Little is known about black rat behavior in macadamia orchards. The abundance and availability of nuts vary seasonally, probably influencing the density, home ranges, and movements of rats in orchards. More knowledge about the daily and seasonal activity and movements of rats in macadamia orchards could help determine the optimum density and spatial and temporal distribution of traps, rodenticide baits, or other measures used to reduce damage.

We conducted this study to 1) describe the nightly movements of rats in a macadamia orchard, 2) examine seasonal differences in these movements, and 3) relate any seasonal differences to the abundance and quality of nuts in the orchard.

MATERIALS AND METHODS

Study area

We conducted the study between 13 November 1991 and 15 May 1992 at the Kau Agribusiness, Inc., Mauna Loa Macadamia Nut orchard in Keaau, about 17 km south of Hilo, Hawaii. The climate is dominated by northeasterly trade winds, mild year-round temperatures that change little from season to season, and mean monthly rainfall that varies from 17 cm in June to 38.5 cm in December. The study orchard was typical of the approximately 2,500 ha of macadamia trees grown on the windward eastern side of the island of Hawaii, an area that contained about 33 % of the state's bearing acreage of this crop. Most mature orchards in this area have large trees with closed canopies and a scarcity of ground vegetation.

The 999-ha Mauna Loa Macadamia Nut orchard consisted of blocks of 15-40 ha each that were separated by 2 dirt roads and a double-row windbreak of Norfolk Island pines (*Araucaria heterophylla*). The orchard floor consisted of porous lava rock overlain with 8-15 cm of soil and sparse, irregularly distributed weeds. We conducted the study in an interior 21-ha block that contained 240 trees per hectare (6.5 m \times 6.5 m spacing). Ninety-four percent of the study block contained trees that were 20 years of age, nut-bearing, and 8-10 m tall with interlocking canopies. About 4 % of the block contained young replants for wind-damaged, diseased, or dead trees. The remainder of the block comprised empty spaces where trees had died.

The study block contained 3 varieties of macadamia trees: 660 (86.2 %), 508 (9.1 %), and 344 (4.7 %) (Hamilton and Ito 1984). Variety 508 trees were interspersed evenly throughout the block to serve as a pollinator for variety 660; variety 344 comprised mostly young, non-bearing trees scattered throughout the block as replacements for dead trees.

Methods

We monitored movements of adult black rats from 21 November to 6 December 1991, 27 January to 14 February 1992, and 27 April to 15 May 1992. These periods coincided with 3 stages of the crop cycle : 1) peak harvest, when most nuts were full-grown, high in fatty acids, and surrounded by hard shells and husks ; 2) peak anthesis, when flowering was at a maximum and mature, full-grown nuts were scarcest ; and 3) mid-way through the 1992 season (60-100 days after peak anthesis), when most nuts were approaching full size, but were still low in fatty acids and lacking fully formed shells and husks. The terms « peak harvest », « peak anthesis », and « midseason » in this study refer to variety 660.

During each period, we secured Haguruma® live traps to lower lateral branches in macadamia trees, as well as on the ground in surrounding windbreaks (reference to commercial products for identification purposes does not imply endorsement by the authors or the U.S. Department of Agriculture). We did not attempt to capture rats on the ground inside the orchard because previous efforts to do so were unsuccessful (Tobin *et al.* 1993). We fastened traps open and prebaited them with chunks of coconut for 3-4 days before setting them with fresh coconut and monitoring them daily for 7-9 days. We anesthetized rats by placing traps with captures into a plastic container lined with cotton soaked in methoxyflurane. We weighed anesthetized rats, determined their gender, and attached standard 164-167-MHz collar radio transmitters with whip antennae (Advanced Telemetry Systems, Inc.®). Transmitters had a mass of 6 g and a battery life of 4 wk. We released rats at the point of capture and observed them until they recovered and moved away into the canopy or a burrow.

Beginning 3-4 days after completion of trapping, we monitored nightly movements of rats for 3 nights during each of the following 3 wk. During each of the 9 nights, we recorded locations of collared animals at 2-hour intervals between sunset and sunrise. We also took readings at various times between sunrise and sunset to locate daily resting places. Observers with head-lamps, portable radio receivers (Custom Electronics of Urbana Inc.®), and hand-held Yagi antennae (Wildlife Materials®) walked through the orchard and located the source of each transmitted signal. Prior to the study, each observer practiced until he or she could accurately locate the source of signals emanating from investigator-placed transmitters in trees, on the ground, or in burrows. The order in which we tracked the rats was uniform during the course of any given night. However, we started with a different animal each night so that we did not always monitor the same rats during those periods shortly after sunset and before sunrise. For each rat, we recorded observer, date, time, receiver, tuning and signal strength, row and number of the tree closest to the source of the signal, position of animal (tree, ground, or burrow), activity (moving or stationary), visual confirmation (yes/no), weather conditions (wind speed, rain, cloud cover), and phase of moon.

We used Micro-computer Programs for the Analysis of Animal Locations (McPAAL ; M. Stuwe and C.E. Blohowiak, Conservation and Research Center, National Zoological Park, Smithsonian Institution) to calculate the home range size for each rat by the minimum convex polygon (MCP) method. We also calculated the median distance from center of activity (MDIS) for each rat to estimate its nightly and seasonal movement distances. We calculated the MDIS as the median distance of all locations for an animal from its center of activity (mean x and y coordinates of all locations) (SAS Institute Inc. 1988). We calculated a Pearson product moment correlation to determine whether MCP and MDIS were correlated with each other and with sample size. We performed a 2-way ANOVA to compare home range sizes between sexes and

among seasons. We performed a paired t-test for each period of the crop cycle to compare the proportion of in-tree locations for individual rats that were in variety 660 to 90% (the percentage of bearing trees in the study block that comprised that variety).

We grouped daily activity into 8 periods: (0701-1700 hours, 1701-1900 hours, 1901-2100 hours, 2101-2300 hours, 2301-0100 hours, 0101-0300 hours, 0301-0500 hours, 0501-0700 hours). We divided the moon into 4 phases: full (the 7 dates centered on the date of the full moon), waning (the period between the full and new moons), new (the 7 days centered on the date of the new moon), and waxing (the period between the new and full moons). We performed separate ANOVA's for each period of the crop cycle to compare the percentage of animals out of burrows among times of day and phases of the lunar cycle; we used Duncan's multiple range test with an experiment-wise error rate of 0.05 to make multiple comparisons (Saville 1990).

We captured, handled, and anesthetized rats according to approved U.S. Department of Agriculture, Denver Wildlife Research Center standard operating procedures and animal welfare standards.

RESULTS

We trapped and radio-collared 18 rats during peak harvest, 25 rats during peak anthesis, and 27 rats during midseason. Some rats died or lost their transmitters during the study, as evidenced by stationary signals emanating from underground burrows. The lava substrate precluded us from recovering most of these transmitters and verifying the cause. Transmitter failure also prevented us from monitoring some rats. We analyzed data only for rats that we tracked for at least 6 nights over a period of ≥ 11 days: 17 rats during peak harvest, 19 rats during peak anthesis, and 18 rats during midseason.

Fidelity to capture location

We captured 51 rats in the orchard and 3 rats in the windbreak. We observed only 2 of the rats initially captured in the orchard outside of the study block: 1 rat on 3 occasions and another rat once. Two rats that we initially captured in the windbreak remained there during all of our observations: on 4 occasions we located the third rat captured in the windbreak in adjacent macadamia trees.

Home range and movement distances

Radio collared rats had an average body mass of 125 g (SE = 4.1); all rats except 6 had a body mass ≥ 90 g. Neither MCP areas nor MDIS differed between the 6 rats that had a body mass < 90 g and the 48 rats that had a mass ≥ 90 g (MCP: $t = 0.30$, 52 df, $P = 0.76$; MDIS: $t = 0.16$, 52 df, $P = 0.87$). When we ranked the 54 radio-collared rats according to MCP size and MDIS, the 6 rats with a body mass < 90 g had a mean ranking of 27 and 28, respectively.

MCP home range measures and MDIS estimates were correlated ($r = 0.30$, $P = 0.03$, 53 df). Neither MCP nor MDIS estimates were related to sample size (r ranged from 0.001 to 0.20, 53 df, $P > 0.20$.) or varied among crop periods or between sexes. Mean MCP home ranges for males and females combined ranged from 1,811 m² to 2,105 m² among the 3 periods of the macadamia crop cycle ($F = 0.62$; 2,48 df; $P =$

0.54) (Table 1). Pooled across seasons, mean MCP home range measured 2,203 m² for males and 1,803 m² for females ($F = 1.93$; 1, 48 df; $P = 0.17$) (Table 1). Mean MDIS for both sexes combined ranged among the 3 periods of the crop cycle from 13.3 m to 16.5 m ($F = 2.38$; 2, 48 df; $P = 0.10$), or about 75 % of the distance between 2 trees (Table 1). Mean MDIS for all seasons combined was 15.2 m for males and 15.6 m for females ($F = 0.20$; 1, 48 df; $P = 0.66$).

TABLE 1. – Mean minimum convex polygon home range sizes and median distances moved from center of activity of *Rattus rattus* in a Hawaiian macadamia orchard during 3 periods of the crop cycle, 1991-1992.

Sex	N	Minimum convex		Median	
		polygon (m ²)		distance (m)	
		Mean	SE	Mean	SE
Harvest, 1991					
male	8	1930	337	11.5	1.6
female	9	1705	420	14.9	1.9
all rats	17	1811	266	13.3	1.3
Anthesis, 1992					
male	10	2239	333	16.0	2.0
female	9	1632	337	17.2	3.1
all rats	19	1952	241	16.5	1.8
Midseason, 1992					
male	3	2813	730	22.3	5.4
female	15	1963	451	15.0	1.4
all rats	18	2105	395	16.2	1.5
Pooled Seasons					
male	21	2203	225	15.2	1.5
female	33	1803	247	15.6	1.1
all rats	54	1959	179	15.4	0.9

Location of activity

All locations of radio-collared rats were either in trees or in underground burrows. We detected no activity on the surface of the ground. During all phases of the crop cycle, above-ground activity was lowest between 0701 and 1700 hours (Fig. 1). Rats were in burrows during 85.0 % (SE = 6.0) of peak harvest day readings (0701-1700 hours), 84.7 % (SE = 6.3) of peak anthesis day readings, and 93.0 % (SE = 5.0) of midseason day readings. Thirty-four rats utilized underground dens exclusively during the day; we never observed them in the canopy between 0701 and 1700 hours. Individual animals resided under the same or adjacent trees (probably interconnected by sub-

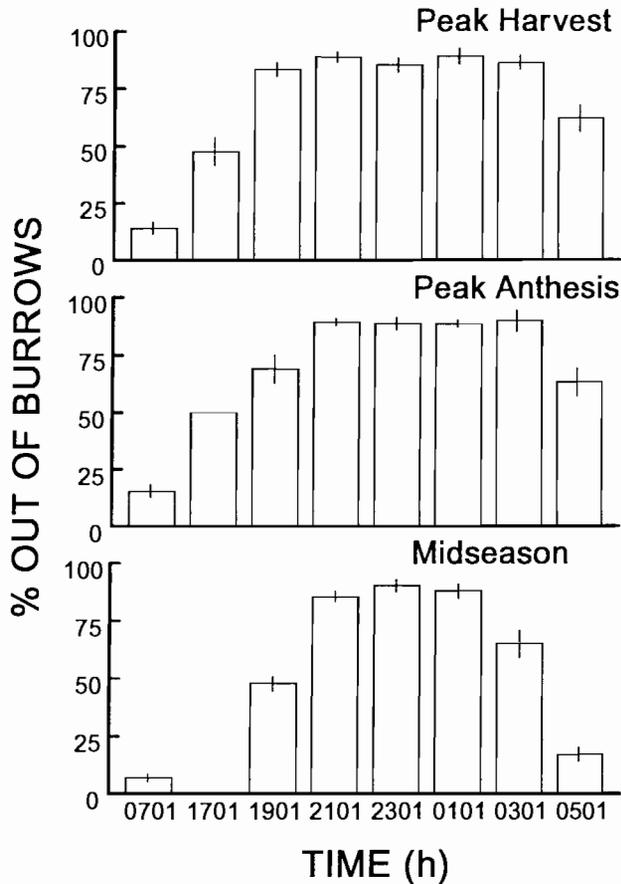


Fig. 1. – Mean percentage of *Rattus rattus* outside burrows in a Hawaiian macadamia orchard during different times of day and periods of the crop cycle, 1991-92. The first bar to the left of each group represents the period from 0701-1700 hours. The remaining bars represent successive 2-hour periods between 1701 and 0700 h. Lines above bars represent SEs of the means. We did not monitor rats between 1701 and 1900 hours of midseason.

terranean cracks and crevices that permeated the lava rock substrate) during 85 % (SE = 2.7) of the day readings. Twenty rats resided in the canopy during ≥ 1 day reading, but only 2 rats each from peak harvest and peak anthesis and 1 rat from midseason utilized the canopy during > 50 % of the day readings. We detected canopy nests for 1 female and 3 males out of the 5 rats that used primarily arboreal denning sites.

Circadian pattern of activity

Rats typically emerged from their burrows 1-2 hours after sunset, ascended into the canopy, and returned to their burrows 1-2 hours before sunrise (Fig. 1). Because of the later sunsets during peak anthesis and midseason, we delayed recording nightly locations until after 1900 hours during all but 4 nights of these 2 periods. During each

period of the crop cycle, the mean percentage of rats out of their burrows was less ($P < 0.05$) between 0701 and 1700 hours (7-15 %) than during any time between 1901 and 0500 hours (48-90 %).

Lunar phases and nightly activity

Nightly activity depended on the phase of the moon during peak harvest ($F = 2.90$; 14, 48 df ; $P = 0.0031$) and peak anthesis ($F = 2.38$; 12, 42 df ; $P = 0.0191$), but not midseason ($F = 1.16$; 18, 34 df ; $P = 0.34$). During peak harvest, activity was lower ($P < 0.05$) between 0501 and 0700 hours of a full or waning moon (still up around sunrise) than at any other time of night (Fig. 2). During peak harvest, activity also was less

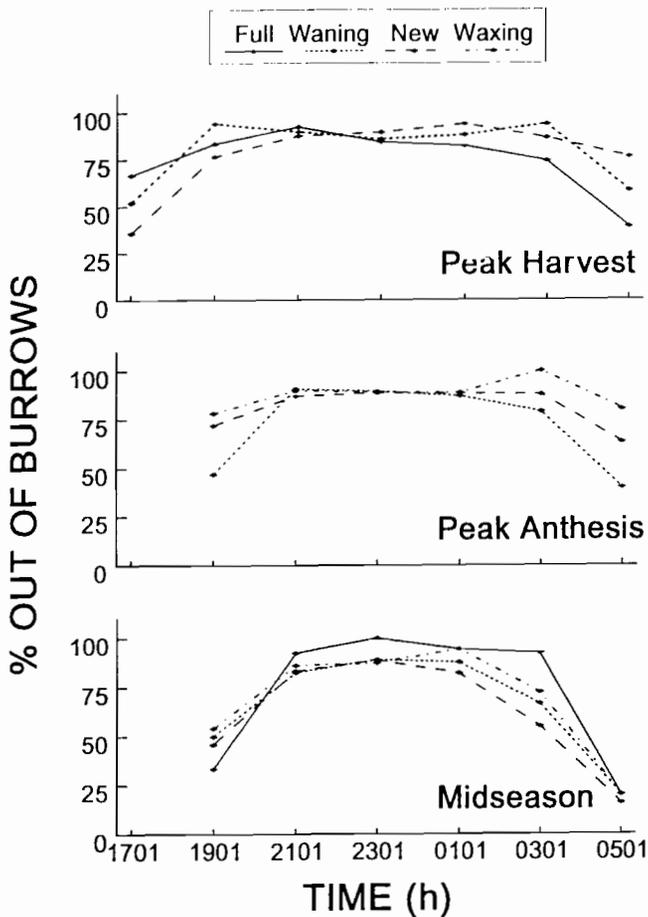


Fig. 2. – Percentage of *Rattus rattus* outside burrows in a Hawaiian macadamia orchard at different times of night and phases of the moon during three periods of the crop cycle, 1991-92. We did not monitor rats between 1701 and 1900 hours during all moon phases of peak anthesis and midseason, and therefore, omitted observations from these periods.

($P < 0.05$) around sunset (1701-1900 hours) of a new (up around sunset) or waning moon relative to the rest of the night. During peak anthesis, relatively fewer ($P < 0.05$) rats were above ground between 1901 and 2100 hours of waxing (still up at sunset) and waning moons than during any other period between 1901 and 0500 hours (Fig. 2). Above-ground activity during midseason varied independently with time of day ($F = 89.35$; 6, 34 df; $P = 0.0001$) and lunar phase ($F = 2.84$; 3, 34 df; $P = 0.0526$). During midseason, activity was greater ($P < 0.05$) between 2101 and 0300 hours than at any other time of night, greater between 0301 and 0500 hours than between 1901 and 2100 hours or 0501 and 0700 hours, and greater between 1901 and 2100 hours than 0501 and 0700 hours (Fig. 2). None of the pairwise comparisons among moon phases was significant ($P > 0.05$).

Precipitation

Total precipitation on the dates we monitored rats exceeded 29.9 cm during peak harvest, 2.7 cm during peak anthesis, and 12.8 cm during midseason. We saw no evidence of a relationship between rain and nightly activity. The mean percentage of night readings (1901-0500 h) that were of rats in trees was 80.6 % when it rained and 82.5 % when it did not ($t = 1.9$, 53 df, $P = 0.31$).

Tree variety

The harvest season for variety 508 was longer than that for variety 660; nut fall for the former variety extended throughout most of the year. During peak harvest, when the abundance of mature 660 nuts was greatest, a mean of 95 % of canopy locations for individual rats were in variety 660. This was greater than the percentage of all mature trees in the orchard that were this variety (90 %) ($t = 2.98$, 16 df, $P = 0.009$). The mean percentage of canopy readings in variety 660 did not differ from the overall occurrence of this variety during peak anthesis (86 %, $t = 1.50$, 18 df, $P = 0.15$) or midseason (85 %, $t = 1.23$, 17 df, $P = 0.23$).

DISCUSSION

Our study site was typical of mature macadamia orchards on the eastern, windward side of Hawaii island and was ideal, albeit very specialized, habitat for black rats. Most trees were ≥ 20 years of age and had dense, interlocking canopies that allowed rats to move among trees. The lava substrate beneath the orchard floor, permeated with cracks and crevices, provided nesting and denning sites and facilitated subterranean movement. A prolonged macadamia flowering season and extended nut maturation period resulted in an almost continuous availability of nuts (Cavaletto 1983) that allowed rats to subsist and breed year-round on a diet composed almost entirely of macadamia nuts (Tobin *et al.* 1994). The small home ranges of rats within the orchard confirmed that rats did not have to travel far to acquire daily nutritional requirements.

Several previous studies indicate that black rats from a variety of non-commensal habitats and geographical locations have restricted movements and limited dispersal. Black rats captured, marked, released, and recaptured in Ponape, Micronesia, had mean home ranges of 0.33 ha in grasslands, 0.16 ha in a rain forest, and 0.12 ha on a coconut plantation (Jackson and Strecker 1962). In a Californian riparian woodland, black rats

had a mean home range of 0.19 ha (Stroud 1982). In New Zealand, home ranges averaged 0.12 ha in a mixed podocarp (*Podocarpus* spp.)-rata (*Metrosideros umbellata*)-broadleaf forest (Daniel 1972), 0.85 ha in a kauri (*Agathis australis*) forest (Dowding and Murphy 1994), and 0.54 ha in a rata-kamahahi (*Weinmannia racemosa*) forest (Hickson *et al.* 1986).

Studies from non-macadamia habitats in Hawaii also indicate that black rats move limited distances. In a semi-mountainous brushy field on Oahu, black rats remained within an area with a diameter of about 60 m (Spencer and Davis 1950). In a kiawe (*Prosopis pallida*) forest on the windward side of Oahu, black rats moved about 18 m between recapture points (Tamarin and Malecha 1971). Male and female black rats captured repeatedly in sugarcane fields and adjacent uncultivated areas on Hawaii island moved an average of 27 m and 22 m, respectively, during 4 nights of trapping, and 40 m and 26 m, respectively, during > 1 month (Tomich 1970).

We found little evidence that home ranges varied between males and females. As in our study, males in most of the studies cited above (Spencer and Davis 1950, Tomich 1970, Daniel 1972, Stroud 1982, Dowding and Murphy 1994) moved slightly, but not significantly ($P > 0.05$), farther than females during their daily movements.

We initially hypothesized that home ranges would expand during times of relative nut scarcity (e.g., during peak anthesis) because rats presumably must travel farther to find food. However, home ranges varied little among periods of the crop cycle. The disproportionate number of rat locations in variety 660 during peak harvest indicated that rats foraged selectively in trees that had mature or nearly mature nuts.

Most rats in our study remained in the same tree where they were first sighted as their locations were being recorded, but occasionally rats moved to an adjacent tree as the observer approached to within 10-15 m. We recorded the first tree where a rat was detected as the location for that rat. We do not know whether some rats may have been on the ground but scurried into the canopy or into burrows before we approached close enough to detect their original location. However, our low capture success with ground traps and poor acceptance of baits placed on the ground in other studies (Tobin *et al.* unpubl. data) indicate that rats spent little time on the barren orchard floor.

A majority of rats in our study utilized underground burrows exclusively during the day, but 37% denned in trees at least some of the time. Similarly, black rats that foraged in the canopy of Philippine coconut plantations during the night usually returned to the ground during the day (Hoque and Fiedler 1988). However, in around Mediterranean orange groves black rats denned mainly in the canopy (Faus 1990). Studies in a Hawaiian koa (*Acacia* spp.)-ohia (*Metrosideros* spp.) forest (G. Lindsey, U.S. National Biological Service, personal communication), a New Zealand tawa (*Beilschmiedia tawa*)-kohekohe (*Dysoxylum spectabile*) forest (Hooker and Innes 1995), and a Puerto Rican tropical rain forest (Layton 1986) indicate that black rats in uncultivated forests spend much of the night at or near the ground but usually return to the canopy during the day.

Animals in our study remained in their burrows longer after sunset and returned to their burrows sooner before sunrise, respectively, during those times of the lunar cycle when the moon was up around sunset or sunrise. The moon had no apparent effect on above-ground activity during other times of the night. Similarly, rats in a New Zealand forest were active from dusk to dawn, regardless of moon phase or weather, although they sometimes stopped moving during heavy rain (Hooker and Innes 1995). Various rodents that inhabit open desert and scrub habitats alter microhabitat use (Kaufman and Kaufman 1982, Price *et al.* 1984, Wolfe and Summerlin 1989) and activity (Lockard and Owings 1974, O'Farrell 1974, Lockard 1975, Kaufman and Kaufman 1982, Daly *et*

al. 1992) during moonlight and thereby avoid predatory risks. A dense canopy and arboreal habits probably mitigated exposure of the rats in our study to predation by small Indian mongooses (*Herpestes auropunctatus*), barn owls (*Tyto alba*), and domestic cats (*Felis silvestris catus*), the major predators in the study orchard.

CONCLUSIONS

On the eastern, windward side of Hawaii island, rats inhabit macadamia orchards and cause damage during the entire year (Tobin *et al.* 1993). Thus, managers may need to apply damage control measures throughout the crop cycle. The almost total lack of movement between the orchard and the surrounding windbreaks implies that managers should concentrate damage control efforts in the orchard. The most commonly used method for applying rodenticides in Hawaiian macadamia orchards is to broadcast the baits on the orchard floor. The rats' apparent lack of ground activity and relatively small home ranges indicate that effective control may require that growers place baits directly in burrows or trees at ≥ 5 locations/ha. The disproportionately large number of rats in tree varieties with mature or nearly mature nuts indicates that managers may be able to reduce pesticide usage by selectively baiting in such trees.

ACKNOWLEDGMENTS

We are grateful to the Kau Agribusiness Company, Inc. for allowing us to conduct the study in their orchard. D.J. Gusman, E.K. Heidenfeldt, and G.K. Keahloha helped track animals and map animal locations. S.G. Fancy introduced us to the McPAAL software for calculating home ranges. R.M. Engeman provided statistical advice during the study. M.L. Avery, R.M. Engeman, M.W. Fall, and S.G. Fancy reviewed earlier drafts of this manuscript.

BIBLIOGRAPHY

- CAVALETTO, C.G., 1983. – Macadamia nuts. Pp. 361-379, in: *Handbook of tropical foods*. Ed. H.T. Chan, Jr. Marcel Dekker Inc., New York.
- DALY, M., P.R. BEHREND, M.I. WILSON and L.F. JACOBS, 1992. – Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Anim. Behav.*, 44 : 1-9.
- DANIEL, M.J., 1972. – Bionomics of the ship rat (*Rattus rattus*) in a New Zealand indigenous forest. *New Zealand J. Sci.*, 15 : 313-341.
- DOWDING, J.E. and E.C. MURPHY, 1994. – Ecology of ship rats (*Rattus rattus*) in a Kauri (*Agathis australis*) forest in Northland, New Zealand. *New Zealand J. Ecology*, 18 : 19-28.
- FAUS, F.V., 1990. – Vegetal supports for the aerial nesting of Black rat (*Rattus rattus*) in the East of Spain. *Mammalia*, 54 : 147-152.
- FELLOWS, D.P., 1982. – Rat damage and control in macadamia. *Proc. Hawaii Macadamia Prod. Assoc.*, 22 : 94-103.
- HAMILTON, R.A. and P.J. ITO, 1984. – *Macadamia nut cultivars recommended for Hawaii*. Hawaii Institute of Tropical Agriculture and Human Resources, Univ. Hawaii. ISSN 0271-9908, Information Text Series 023. 7 pp.

- HAWAII AGRICULTURAL STATISTICS SERVICE, 1992. – *Hawaii macadamia nuts, final season estimates*. U.S. Dep. Agric., Honolulu. 8 pp.
- HICKSON, R.E., H. MOLLER and A.S. GARRICK, 1986. – Poisoning rats on Stewart Island. *New Zealand J. Ecology*, 9 : 111-121.
- HOOKE, S. and J. INNES, 1995. – Ranging behaviour of forest-dwelling ship rats, *Rattus rattus*, and effects of poisoning with brodifacoum. *New Zealand J. Zool.*, 22 : 291-304.
- HOQUE, M.M. and L.A. FIEDLER, 1988. – *Rat control in coconut*. Tech. Bull. No. 3/1988. National Crop Protection Center, College of Agriculture, Univ. of the Philippines at Los Banos. 20 pp.
- JACKSON, W.B. and R.L. STRECKER, 1962. – Home range studies. Pp. 113-123, in : *Pacific island rat ecology*. Ed. T.I. Storer, Bulletin 225, Bernice P. Bishop Museum, Honolulu.
- KAUFMAN, D.W. and G.A. KAUFMAN, 1982. – Effect of moonlight on activity and microhabitat use by Ord's kangaroo rat (*Dipodomys ordii*). *J. Mamm.*, 63 : 309-312.
- LAYTON, B.W., 1986. – *Reproductive chronology and habitat use by black rats (Rattus rattus) in Puerto Rican parrot (Amazona vittata) nesting habitat*. M.S. Thesis, Louisiana State Univ., Baton Rouge. 98 pp.
- LOCKARD, R.B., 1975. – Experimental inhibition of activity of kangaroo rats in the natural habitat by an artificial moon. *J. Compar. Physiol. Psychol.*, 89 : 263-266.
- LOCKARD, R.B. and D.H. OWINGS, 1974. – Moon-related surface activity of bannertail (*Dipodomys spectabilis*) and Fresno (*D. nitratoides*) kangaroo rats. *Anim. Behav.*, 22 : 262-273.
- PRICE, M.V., N.M. WASER and T.A. BASS, 1984. – Effects of moonlight on microhabitat use by desert rodents. *J. Mamm.*, 65 : 353-356.
- O'FARRELL, M.J., 1974. – Seasonal activity patterns of rodents in a sagebrush community. *J. Mamm.*, 55 : 809-823.
- SAS INSTITUTE INC., 1988. – *SAS/STAT user's guide, release 6.03 ed.* SAS Institute Inc., Cary, NC. 1028 pp.
- SAVILLE, D.J., 1990. – Multiple comparison procedures : the practical solution. *The Am. Statistician*, 44 : 174-180.
- SPENCER, H.J. and D.E. DAVIS, 1950. – Movements and survival of rats in Hawaii. *J. Mamm.*, 31 : 154-157.
- STROUD, D.C., 1982. – Population dynamics of *Rattus rattus* and *R. norvegicus* in a riparian habitat. *J. Mamm.*, 63 : 151-154.
- TAMARIN, R.H. and S.R. MALECHA, 1971. – The population biology of Hawaiian rodents : demographic parameters. *Ecology*, 52 : 383-394.
- TOBIN, M.E., A.E. KOEHLER, R.T. SUGIHARA, G.R. UEUNTEN and A.M. YAMAGUCHI, 1993. – Effects of trapping on rat populations and subsequent damage and yields of macadamia nuts. *Crop Prot.*, 12 : 243-248.
- 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. *Wildl. Res.*, 21 : 519-526.
- TOMICH, P.Q., 1970. – Movement patterns of field rodents in Hawaii. *Pac. Sci.*, 24 : 195-234.
- WOLFE, J.L. and C.T. SUMMERLIN, 1989. – The influence of lunar light on nocturnal activity of the old-field mouse. *Anim. Behav.*, 37 : 410-414.