The habits and interrelationships of rodent species in the Hamakua District of Hawaii are found to be favorable to the perpetuation of enzootic plague.

Observations on Rats in an Enzootic Plague Region of Hawaii

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THE INTERRELATIONS of different rodent species, their survival, movements, feeding habits and, in general, their ability to coexist are fundamental conditions for the maintenance and spread of wild rodent plague. Expert opinion considers that infection per saltum is operative under unusual circumstances, whereas the spread of the disease is primarily by contiguity, probably by "an accumulation of small movements among rodents" (*1*) and by normal dispersal (*2–4*). In a discussion of this problem, Davis (*5*) distinguished between intracolonial and intercolonial spread of plague among South African rodents and concluded that spread by the former method was more usual.

The extent of movement and the home range of small mammals generally has been found to be quite restricted (*6–9*) and the movement rate of *Rattus norvegicus* is known to be very low in constant environments (*10*). Similarly, a study of rats in Hawaii indicated both limited movements and a restricted home range on the island of Oahu (*11*).

A project on methods for the control of fleas on wild rodents inhabiting an enzootic plague region on the island of Hawaii provided observations pertinent to a discussion of the relation of rat characteristics to the perpetuation of wild rodent plague.

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Study Areas and Methods

A detailed description of the study areas and materials and methods employed already has been presented (*12*). The work, which was concerned primarily with wild rodent flea control, was conducted from February 1952 to May 1953 in a field of sugarcane and in a gulch near the town of Honokaa, Hamakua District, Hawaii. Plague is both enzootic and endemic in this region.

Most of the work was done in Kaunamano gulch, one of numerous ravines bordered by sugarcane fields, grassy slopes, and small cultivated areas. Eighty trapping stations were established within an area of about 4,000 feet in the gulch, where the elevation ran from 400

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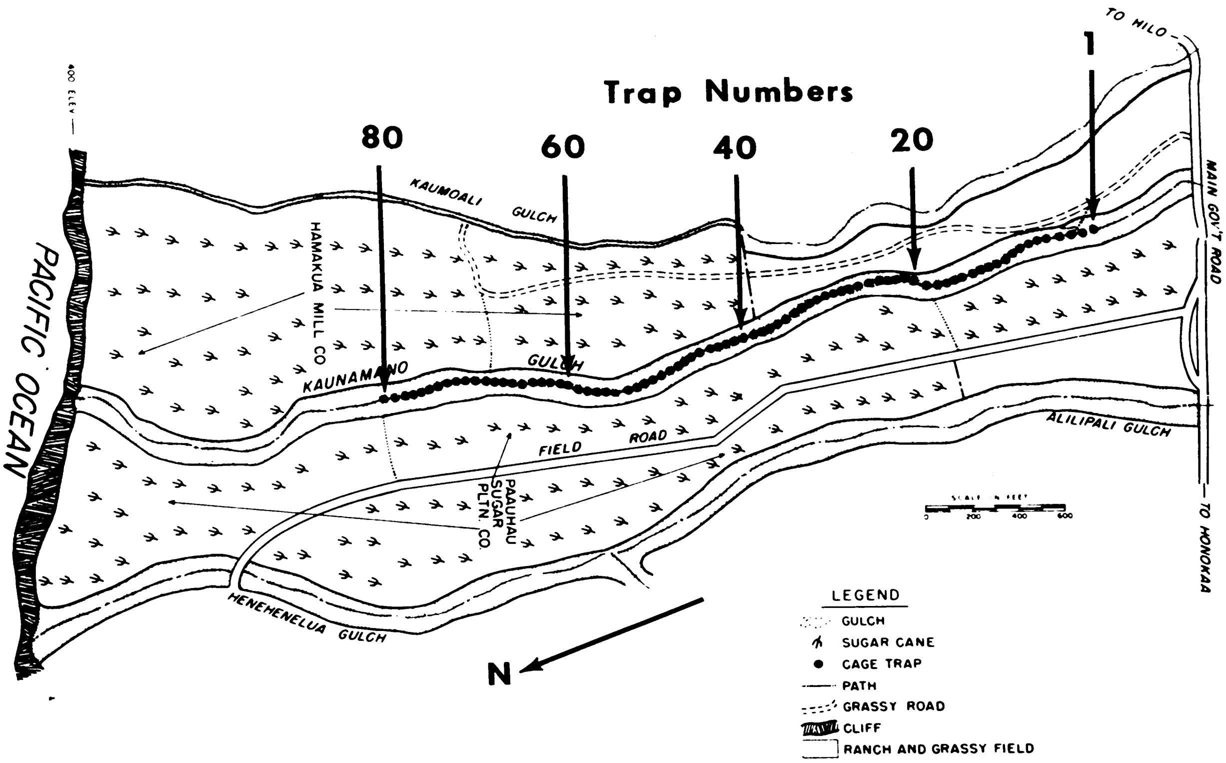
Figure 1. Map of study area in Kaunamano gulch, showing the location of trap sites.



to 750 feet (fig. 1). Each station was supplied with cage traps at 50-foot intervals. The traps were similar to the kind shown in the report by Spencer and Davis (*11*).

At one time during the work, bait boxes were placed at intervals of 5 stations beginning with station No. 1. Rodent activity at these bait boxes was estimated on the basis of bait consumption (*12*) and numbers of fecal pellets. The fecal pellets were counted and the boxes were thoroughly cleaned at each visit.

A small part of the work, lasting about 1½ months, was conducted in a field of sugarcane (field No. 1). This consisted of about 103 acres of mature cane at an elevation of from 200 to 900 feet. An area of approximately 40 to

Table 1. The number of new rats live-trapped by months, in Kaunamano gulch [1]

Species	1952											
	July			August			September			December		
	Number	Percent	Rats per 9 trap-days	Number	Percent	Rats per 8 trap-days	Number	Percent	Rats per 8 trap-days	Number	Percent	Rats per 10 trap-days
Rattus hawaiiensis	33	46. 4	3. 5	22	56. 4	2. 6	21	56. 7	2. 6	40	54. 0	4. 0
Rattus rattus group [2]	36	50. 8	4. 0	14	36. 0	1. 7	13	35. 2	1. 6	23	31. 2	2. 3
Rattus norvegicus	2	2. 8	. 2	3	7. 6	. 3	3	8. 1	. 3	11	14. 8	1. 1
Total rats and ratio per trap-days	71	100	7. 9	39	100	4. 8	37	100	4. 6	74	100	7. 4

50 acres around the periphery of the field was supplied with 200 cage traps at 35-foot intervals.

The traps were baited either with small coconut squares or small pellets made of commercial dog food mixed with rolled oats and wrapped in waxed paper. Rolled barley or rolled oats was used in the bait boxes in amounts that could not be completely consumed between visits.

In a few cases, traps were modified so that an attached clock would be stopped at the moment the trap trigger was released. By setting the alarm in the morning for 8 p. m., the time of capture could be determined by whether or not the alarm spring had unwound.

Captured rats were anesthetized with ether (rarely with chloroform), marked by toe amputation, combed for ectoparasites, checked for pertinent physical data, and released at the point of capture. The results of blood examinations and body temperature determinations have been published elsewhere (*13*, *14*). Individual record cards were kept for each animal captured.

During the course of the major portion of the study, the rats were subjected to the effects of 10 percent DDT powder in pyrophyllite. During October and November 1952 the main effect of warfarin-poisoned oats was studied. The DDT appeared not to have a noticeable influence upon the rats. The warfarin decimated the commensal rat population, and data during this period have been eliminated for purposes of the present report, unless otherwise indicated.

The pressure of other work prevented the use of a grid system of trapping and a more extensive study of the rodents in the plague region. Nevertheless, although the methods employed do not give the detailed results desirable in an investigation of rodent ecology, the data represent a definite contribution to the knowledge of rodent behavior in this region inasmuch as little or nothing has been published in this regard.

Results and Discussion

The four species of rodents found in the Hamakua District are: *Rattus rattus* subspecies *R. r. rattus* and *R. r. alexandrinus; Rattus norvegicus; Rattus hawaiiensis*, and *Mus musculus*. For present purposes, all subspecies of *R. rattus* are considered together and no data are presented on the house mouse. All of these species live wild in the field, but the native rat, *R. hawaiiensis*, is the only truly wild rodent in Hawaii—it lives only in the field and never in human habitation.

The number of rats of each species trapped during each month in Kaunamano gulch is shown in table 1. The predominance of *R. hawaiiensis* and *R. rattus* in this region corroborates a former study (*15*). The average number of rats of all species per acre in gulch areas of the Hamakua District has been estimated at

Table 1. The number of new rats live-trapped by months, in Kaunamano gulch [1]—Continued

Species	1953											
	January			February			March			April		
	Number	Percent	Rats per 5 trap-days	Number	Percent	Rats per 7 trap-days	Number	Percent	Rats per 13 trap-days	Number	Percent	Rats per 14 trap-days
Rattus hawaiiensis	40	76. 9	8. 0	38	66. 6	5. 4	109	48. 6	8. 3	132	55. 9	9. 4
Rattus rattus group [2]	11	21. 2	2. 2	7	12. 2	1. 0	96	43. 0	7. 3	65	27. 6	4. 6
Rattus norvegicus	1	1. 9	. 2	12	21. 2	1. 7	19	8. 4	1. 4	39	16. 5	2. 7
Total rats and ratio per trap-days	52	100	10. 4	57	100	8. 1	224	100	17. 2	236	100	16. 8

[1] Excludes data for October 1953, when the effects of warfarin poisoning on the *rattus* group population were obvious: *R. hawaiiensis*, 21; *R. rattus* group, 4; *R. norvegicus*, 3.
[2] *Rattus rattus rattus* and *Rattus rattus alexandrinus*.

between 40–60 (*15*). Application of the Lincoln index (*16*)

$$\frac{\text{animals marked in precensus period}}{\text{other animals present in precensus period}} = \frac{\text{marked animals trapped in census period}}{\text{other animals trapped in census period}}$$

to some of the data recorded here showed, for example, that the estimated total populations of all rat species in the gulch study area during the periods July–August 1952 and January–February 1953 were respectively, 182 and 223. The actual number of captures of all rat species made during these periods was respectively, 110 and 109.

In another report (*12*), the commensal rat species, primarily *R. rattus*, were shown to be the predominant populations feeding at the bait boxes. The report also showed that bait consumption could be maintained at an almost constant level in the manner shown by Chitty for *R. norvegicus* (*17*). The counting of fecal pellets may also provide a means of determining the population level (fig. 2). The generally greater abundance of small fecal pellets suggests that young individuals predominated among rats feeding in the bait boxes.

Rolled barley was used from the first baiting on May 21 to July 2. During this time the fecal pellet curve rose to a maximum and leveled off. However, on July 3 the bait was changed to rolled oats. This introduced two new factors—a change in the appearance and odor of the food, and a more highly processed food not requiring the time-consuming task of removing the hulls. Thus, many rats may have been shy of the new food for varying periods, and those that fed did not linger in the bait boxes as long as they had when the rolled barley was used. The result was a sharp drop in the fecal pellet curve which began to rise again as more rats adjusted to the new situation.

Figure 2. The number of fecal pellets removed from bait boxes at each visit and the effect of warfarin poisoning on this measure of rat activity.

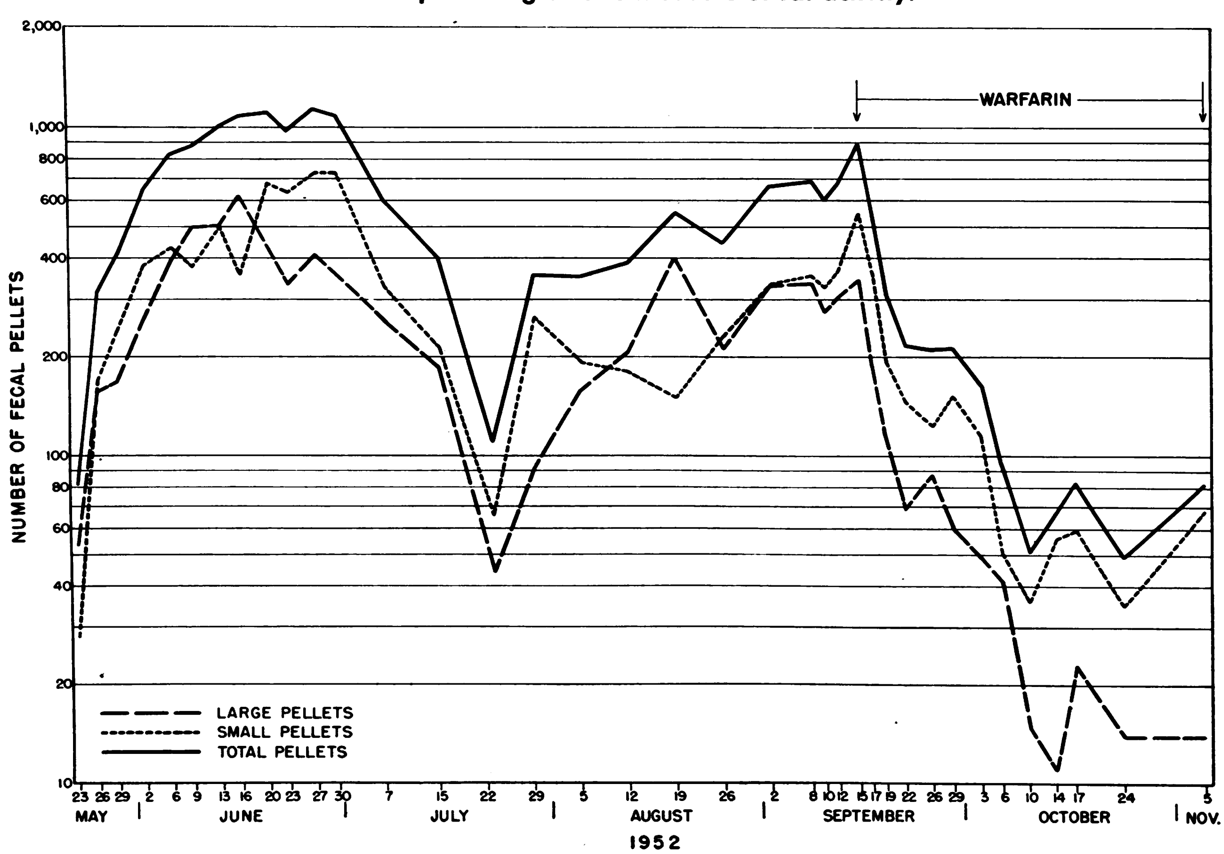


Table 2. Proportion of sexes of live-trapped Rattus species

Location	*R. hawaiiensis*			*R. rattus* group [1]			*R. norvegicus*		
	Male	Female	Ratio	Male	Female	Ratio	Male	Female	Ratio
Field No. 1	25	28	0. 9	25	32	0. 8	10	4	2. 5
Kaunamano gulch	234	222	1. 1	136	133	1. 0	36	57	. 6
Total	259	250	1. 0	161	165	. 9	46	61	. 8

[1] *Rattus rattus rattus* and *Rattus rattus alexandrinus*.

On August 11, a harvest of sugarcane in a field adjacent to the study area was initiated and lasted until August 22. This forced new rats into the gulch area, as was indicated by the trapping, and may be partially responsible for the rising curve of fecal pellets.

Finally, the introduction of warfarin-poisoned rolled oats on September 15 produced the second sharp depression in the curve. These considerations suggest that a controlled count of fecal pellets is a fairly sensitive index of a rat population level as it is influenced by various environmental factors.

No significant differences were found in the proportion of the sexes of the three rat species in either of the study areas (table 2). However, the paucity of *R. norvegicus* did not allow a valid comparison for this species.

Some idea of the survival of the rats can be obtained by an analysis of recaptures, or what amounts to the disappearance of retrappable rats over a period of time (*18*). These data indicate a high probability of disappearance for all three species (table 3). This corroborates findings on the island of Oahu (*11*). The reasons for the high disappearance rate are obscure and appear to contradict the fairly constant level of bait consumption (*12*) and rodent activity (fig. 2). Since an equal number of rats disappeared after their initial capture as were recaptured, some difficulty in retrapping appears to have influenced the results. Among the known factors, the inefficiency of individual traps and frequent springing of traps by mice, *M. musculus*, are probably of importance.

In field No. 1, where trapping lasted less than 2 months, almost 50 percent of the traps failed to capture a single rat, whereas captures of rats in Kaunamano gulch were more consistent (fig. 3). Although the establishment of trap-frequenting orientations by rats over a period of time is undoubtedly a factor in trapping success, the ecological difference between the gulch and field also may have been a factor since 100 percent of the stations became active in the gulch area in less than 2 months (*12*). However, a good deal of variation in success of trapping small mammals has been found to be correlated more with bait attractiveness than with population level (*19*). Thus, the above factors must be considered in an evaluation of rodent survival and other ecological factors.

The coexistence of several rodent species within the same environmental sector is undoubtedly of prime importance for the maintenance of wild rodent plague (*20*), and this idea is implicit in the observations of Eskey (*21*) in his classic study of plague epidemiology in Hawaii. Data published elsewhere have shown that all three rat species in Hawaii may be in-

Table 3. "Survival" of Rattus species in Kaunamano gulch [1]

Month	*R. hawaiiensis*	*R. rattus* group	*R. norvegicus*	Total
Number recaptured	107	58	11	176
1st	77	36	7	120
2d	16	10	1	27
3d	10	8	1	19
4th	2	3	1	6
5th				
6th	1	1	1	3
7th				
8th				
9th	1			1
Not recaptured	103	46	23	172

[1] Data exclude rats found dead, rats first captured during the last 2 months of trapping, and non-*hawaiiensis* taken during the poisoning period.

duced to feed in the same bait box and are hosts to the same species of plague vector fleas and trypanosomes (*12*, *13*). These findings are supported by data on the number of times all species of rats were captured in the same trap (fig. 4).

The number of each rat species attracted to any particular trap generally corresponded to the percentage species composition of the different rat populations in the area (table 1). Although thought to be extremely shy (*22*, *23*), the Hawaiian rat predominated in the majority of trap captures. The probability that the time of feeding does not intervene as a limiting factor in this connection is suggested by a few data on the exact time rats were captured. The available records follow:

R. hawaiiensis		*R. rattus* group		*R. norvegicus*	
a. m.	*p. m.*	*a. m.*	*p. m.*	*a. m.*	*p. m.*
3:30	1:00	3:30	7:45	3:55	
5:17	3:20	4:53	11:30	5:40	
7:10	8:00	5:10	11:40		
	9:50	9:00			
	9:55				

There are enough overlapping times to suggest that many rats of each species undoubtedly seek food in the same area at approximately similar times. Whether or not there is any serious interspecific competition or whether the more aggressive species are predators on the weaker are factors which have not been determined. All three species of rats were found in very close proximity on the island of Maui, and the possibility of predation by *R. rattus* on *R. hawaiiensis* was suggested (*24*).

The Hawaiian rat is thought to be the primary wild plague reservoir from which the other species periodically become infected (*21*, *24*). The possible role of the mouse, *M. musculus*, is not known, but this species was consistently taken in the traps and comprised a large population in the study areas. Thus, in the areas studied, there existed a continuous rodent population composed of the four species mentioned.

Other evidence of the stability and sedentary nature of the rodent populations may be obtained by a study of recapture data and movements of the rats. A summary of these observations is presented in table 4 and examples of individual rat movements are given in table 5. The restricted amount of movement shown for all three species of rats is not surprising inasmuch as these animals would tend to live within

Figure 3. Trapping efficiency as shown by frequency of live captures of rats by traps in: A—Field No. 1, and B—Kaunamano gulch.

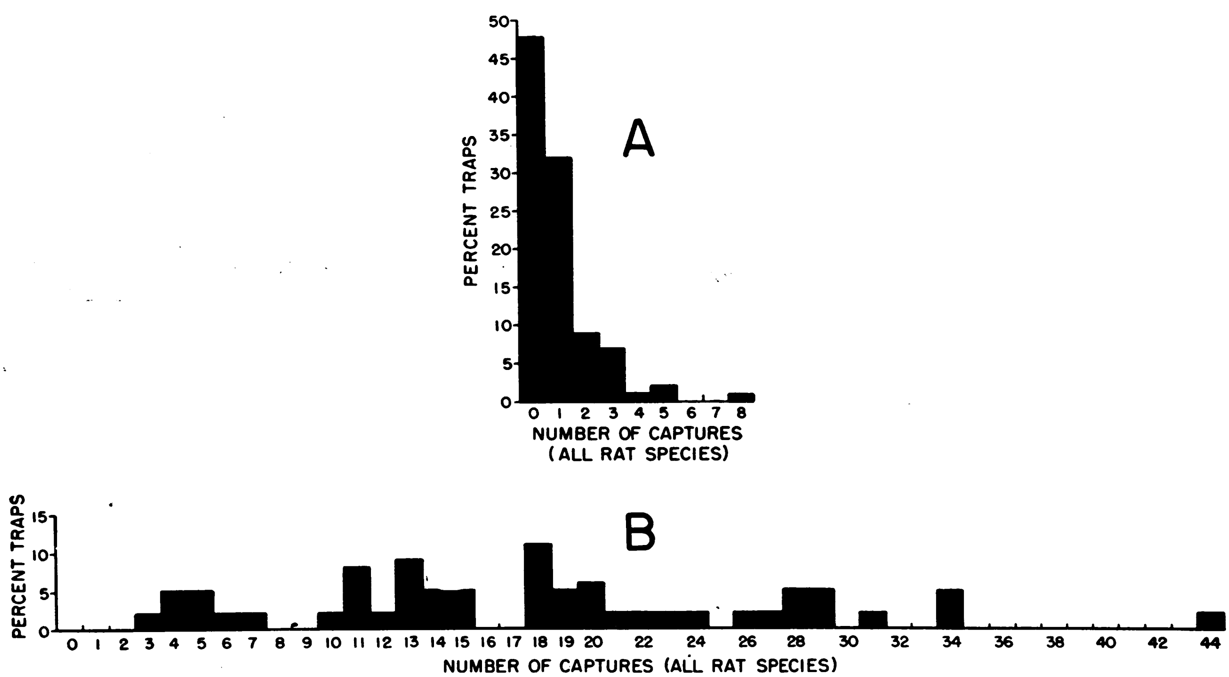
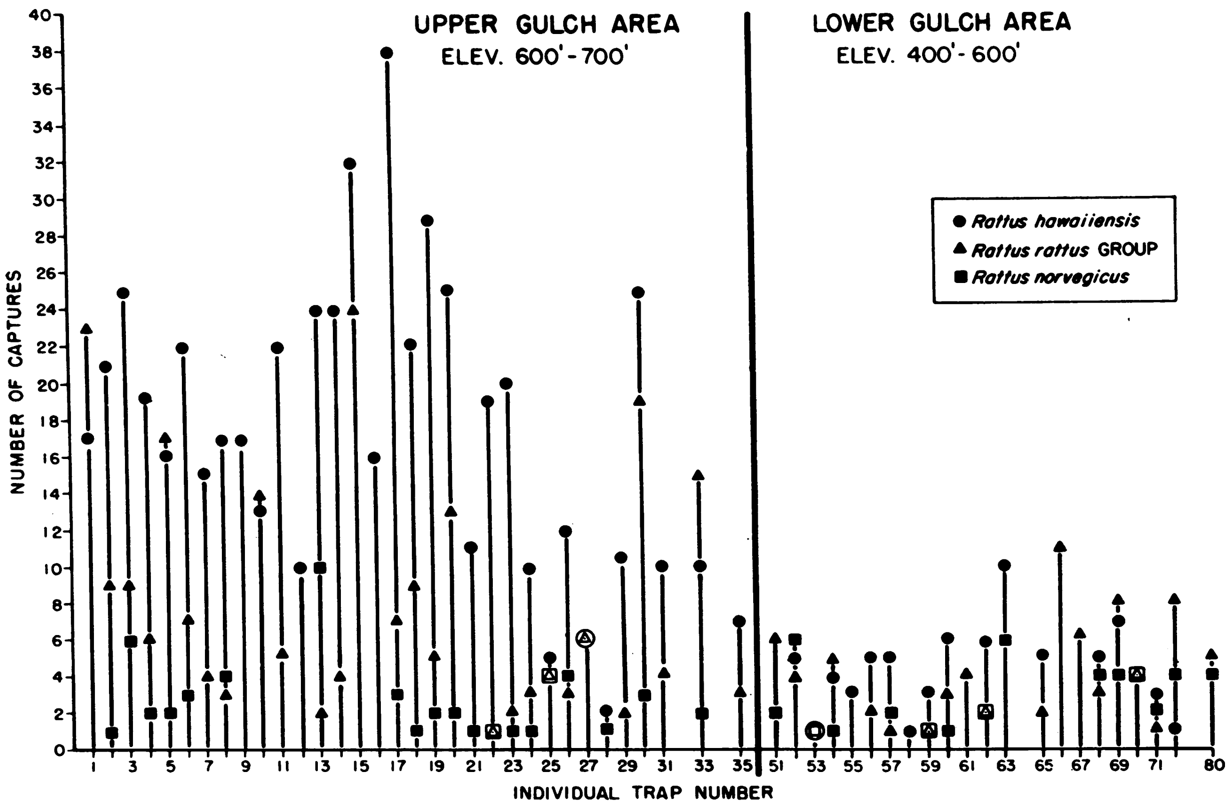


Figure 4. The number of times three species of Rattus were captured alive in the same trap in Kaunamano gulch.



a small area until profound environmental change occurred. Thus, the following percentages of captures were made between 0 and 100 feet from the location of the original capture:

	Field No. 1		*Kaunamano gulch*
Rattus hawaiiensis	74. 1		94. 6
Rattus rattus group	78. 2		80. 5
Rattus norvegicus	28. 5		71. 4
All spp. (both locations)		86. 7	

This indicates predominantly exploratory rather than migratory movement. Few extreme movements were recorded. Two exceptions were: rat No. 130, a female *R. r. alexandrinus*, which was recaptured after 5 months 3,450 feet from the place of original capture, and rat No. 155, a male *R. norvegicus*, recaptured after 6 months 1,500 feet from the site of original capture.

It cannot be asserted that these movement data shed light upon the home ranges of the various rat species since home range is a measure of area. In line with the contentions of Holdenried (*25*), many of the rat movements recorded here are probably measurements of maximal movement which is thought to represent the longest axis of a home range. It must be borne in mind that these so-called maximal movements are determined within the limits set by the arbitrary spacing of traps. In many cases they are probably only fair approximations of the true maximums.

The observations recorded here suggest that, in the region studied, the three species of rats do not carry out extensive migrations, are more or less sedentary populations, and appear to coexist in an environment which favors their close physical proximity with a minimum of adverse interspecific coaction. These characteristics, together with observations already recorded regarding their ectoparasites and disease relationships (*12*, *13*, *21*, *24*), appear to favor the perpetuation of wild rodent plague.

Table 4. Summary data of Rattus spp. recaptures and movements[1]

Type of data	*R. hawaiiensis*		*R. rattus* group[2]		*R. norvegicus*		Totals
	Field No. 1	Kaunamano gulch	Field No. 1	Kaunamano gulch	Field No. 1	Kaunamano gulch	
	Recapture status						
Rats released	53	215	57	107	14	34	480
Not recaptured	35	111	41	48	11	24	270
Recaptured	18	104	16	59	3	10	210
In more than 1 month	4	67	6	36	1	6	110
Dead in traps	3	5	2		2	1	13
	Times recaptured						
Distance (feet) from original capture:							
0	5	120	8	34		4	171
1–49	10	63	6	17	1	3	100
50–99	5	11	4	7	1	3	31
100–149	4	2	2	2			10
150–199	1		1	4		2	8
200–249		1	1	2	1	1	6
250–299		1		2	1		4
300–349	2	2	1	1			6
350–399		2					2
400–449		3		1	1	1	6
450–499				1	1		2
650–699				1	1		2
Total	27	205	23	72	7	14	348

[1] These data include only a portion of the total rats captured (see table 1).
[2] *Rattus rattus rattus* and *Rattus rattus alexandrinus.*

Table 5. Examples of individual rat movements in Kaunamano gulch

Species and rat No.	Age	Sex	Location[1] of capture (station No.)									
			1952						1953			
			July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
R. hawaiiensis:												
42	Juvenile	F	23	22		22						
1	Adult	F	3	3		3						
70	Juvenile	F	2								1	2
152	Adult	M				20					18	18
72	Adult	M						19	19	19	20	20
71	Adult	F						15	15	17	16	
R. rattus group:												
25	Adult	F	29	30	30							
44	Adult	M	15	18	18							
16	Adult	M						18	17			17
50	Adult	F						14	15			15
130	Adult	F			80						11	
R. norvegicus:												
10	Juvenile	F						13		13		
17	Juvenile	F						13				17
155	Adult	M				6						35

[1] See figure 1 for location of station numbers.

Summary

Observations are reported concerning wild rodents inhabiting areas within an enzootic plague region on the island of Hawaii. The rat species *Rattus hawaiiensis*, *Rattus rattus* subspecies, and *Rattus norvegicus* were captured alive, marked, released, and recaptured to gain some idea of their survival, movements, and interrelations. Results suggested that none of the rat species migrates extensively, that they constitute more or less sedentary populations, and that they appear to coexist in an environment which favors their close physical proximity. Thus, in the areas studied, there appears to be a continuous rodent population having characteristics favorable for the perpetuation of wild rodent plague.

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