

## The Ecology of *Rattus exulans* (Peale) Reviewed<sup>1</sup>

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**ABSTRACT:** Several aspects of the ecology of *Rattus exulans* are reviewed in an effort to collate a large proportion of the widely scattered literature relating to the species. Subspecific relationships are discussed to illustrate the early confusion regarding taxonomic position. Literature covering *R. exulans* geographic distribution, habitat, nutrition, reproduction, movements, and competition with other species of *Rattus*, is reviewed and discussed.

*Rattus exulans* probably ranks third in the genus for extent of geographic range and is of interest from both academic and economic viewpoints. The species occurs on nearly every Pacific island that lies within 30 degrees of the equator and has extended its range south to include New Zealand. It is thought to have spread in association with Polynesian colonization. Of particular interest is the species' secondary modification of range and habitats as a result of competition with other members of the genus, particularly *Rattus rattus* (Linnaeus) and *Rattus norvegicus* (Berkenhout). The Polynesian rat causes damage of considerable economic importance in some areas of the Pacific and Southeast Asia, primarily to coconuts, sugarcane, and rice. It is also an important vector of the typhus-carrying mite and of the plague flea in some areas (Audy and Harrison, 1951; Elbel and Thaineua, 1957).

This review attempts, within the limits of available literature, to collate data concerning the past and present ecology of the species. The literature of *R. exulans* relevant to Hawaii has been well reviewed by Tomich (1969: 36 and 124) but an assembly of other literature seems in order. Few studies have been devoted to the Polynesian rat alone, most having been made in conjunction with investigations of other members of the genus; some have been a part of studies which were specifically aimed at rodent control. It is hoped that the collation of a section of the data relevant to the species will be of use to other workers in the field.

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### SUBSPECIFIC RELATIONSHIPS

At least five names have been assigned to Pacific island rats as they were successively discovered on widely separated small islands. They are, *Mus exulans* Peale (1848), Tahiti; *Mus vitien-sis* Peale (1848), Fiji; *Mus maorium* Hutton (1877), New Zealand; *Mus jessoock* Jentink (1879), New Hebrides; and *Mus huegeli* Thomas (1880), Fiji. All these species are considered to be synonymous with *Rattus exulans* (Peale), by Tate (1935), but he considered *Rattus hawaiiensis* Stone (1917) and *Rattus micronesiensis* Tokuda (1933) to be distinct species. More recent authors (Ellerman, 1947; Marples, 1955; and Johnson, 1962) considered the latter two species to be of subspecific or race rank. Ellerman (1947) listed 12 races of *R. exulans* including *exulans*, *concolor*, *browni*, *ephippium*, *aemuli*, *negrinus*, *surdus*, *todayensis*, *vulcani*, *stragulum*, *raveni*, and *hawaiiensis*. Johnson (1962) considered *R. micronesiensis* to be a subspecies of *R. exulans*.

The present review will follow the opinions of Ellerman, Marples, and Johnson by including all races and subspecies mentioned as members of the species *R. exulans*.

### GEOGRAPHIC DISTRIBUTION

*R. exulans* has a wide geographic range, but within the range distribution is disjunct. The dispersal of the species east of Indonesia is thought to have been in association with human dispersal (Tate, 1935), though the suggestion that rats were deliberately conveyed is discounted by Shapiro (cited in Tate, 1935, as a personal communication). It is believed that

the species arrived in New Zealand with Polynesians migrating from the Cook Islands. Maori tradition claims the arrival of the *kiore* (Maori name for *R. exulans*) in the canoe Horouta, one of the Great Fleet, about A.D. 1350 (Buck, 1949).

*Rattus exulans* appears to have been abundant in most areas occupied in the Pacific prior to the arrival of *R. norvegicus* 100 to 150 years ago. This was apparently the case in New Zealand where it is considered to have been an important food of the Maori (Wodzicki, 1950). As early as 1835, however, *R. exulans* is thought to have been replaced by *R. norvegicus* in northern Auckland (Darwin, 1845) and by 1840 was reported to be rare over much of the North Island (Gray, 1843). In the South Island the species (identified by Buller, 1893) remained prevalent up to about 1900, and periodic plagues were reported in the Nelson Marlborough districts (Meeson, 1884; Hutton, 1887). Thomson (1922) considered *R. exulans* to be extinct in New Zealand; however, Stead (1936) reported *R. exulans* on Taranga (Hen Island). It has since been found on several islands along New Zealand's northern shores as well as Doubtful Sound, Notornis Valley, Stewart Island, and Hidden Island (Watson, 1956).

Numerous authors (Dixon, 1878; Ivens, 1927; Cook, 1789 [cited in King, 1955]; Stetson, 1854 [cited in Howland, 1955]; Martin, 1827; Stair, 1897; and Woodford, 1895) during the late 19th and early 20th centuries reported "polynesian rats" to be abundant, and often troublesome, in the Pacific region. Today *R. exulans* shares most of its Pacific habitats with at least one other member of the genus. In 1940 Heyerdahl reported *R. exulans* to be the only rat present on Faturiva in the Marquesas Islands, whereas Wodzicki found the same situation in the Tokelau Islands in 1967. In the period 1966 to 1969 Smith (1969) found numerous islands in the Gilbert and Ellice group to be occupied by *R. exulans* only.

#### HABITAT

In Hawaii Bianchi (1961) and Kami (1966) found *R. exulans* and *R. rattus* occupying gulches adjacent to sugarcane fields in equal numbers.

On Ponape in the Caroline Islands, Strecker and Jackson (1962a) found *R. exulans* to be the dominant species in the three habitats studied (rain forest, grassland, and coconut plantations with good ground cover) with the highest densities occurring in the coconut plantations. Baker (1946) found that *R. exulans* on Guam, Mariana Islands, prefers well-drained regions in grasslands and coconut areas and avoids undisturbed coral jungles and villages. Nicholson and Warner (1953) found similar habitat preferences in New Caledonia but considered the numbers of *R. exulans* present in some habitats to be determined by the population densities of the larger *Rattus* species.

The only general trend in habitat choice in the Pacific region seems to be a preference for areas with good ground cover on relatively dry, or at least well-drained, soil. *R. exulans* appears to be found in human habitations in the Pacific only when other *Rattus* species are absent. This situation contrasts with that found on the Malayan peninsular where this species is often found in human dwellings, despite the presence of numerous other species (Harrison, 1957; Searle and Dhaliwal, 1957).

*R. exulans* does not seem to occupy virgin jungle in either the Pacific or the Malayan region, probably because of unfavorable conditions on forest floors where the ground is damp (Marples, 1955; Harrison, 1957). Further aspects of habitats are considered in the discussion on interspecific competition.

#### NUTRITION

Only a few investigations of the diet of *R. exulans* have been carried out. Fall, Medina, and Jackson (1971), who studied the contents of 83 stomachs from rats collected on Eniwetok atoll, have provided the most recent and detailed information. Using microtechniques, they calculated the frequency of occurrence and percentage of materials present. Plant foods were predominant in the diet, with two species (*Scaevola* and *Tournefortia*) accounting for 80 percent of the diet on a weight basis. The predominance of these two species in the diet is a reflection of their being the most abundant shrubs in virtually all the habitats on the atoll.

Insect parts constituted a small fraction of the stomach contents on a weight basis; they occurred in less than 10 percent of the stomachs of *R. exulans*.

Kami (1966), like Fall et al. (1971), confirmed the general observations of Baker (1946), Strecker and Jackson (1962a), and Marples (1955) who found that about 90 percent of the diet consisted of vegetable matter and the remaining 10 percent, of invertebrate or vertebrate material. Kami, studying *R. exulans* captured in sugarcane fields, found, on a percentage volume basis, that 67.2 percent of the food of these rats consisted of sugarcane, 15.1 percent of seeds and grass stalks, and 7.5 percent of insects, other invertebrates, and vertebrates. Gulch-inhabiting rats also ate sugarcane (51.5 percent of stomach volumes). The other two categories totalled 17.1 percent and 5.9 percent, respectively.

Analyzing 46 stomachs from three habitats, Strecker and Jackson (1962a) found that plant material comprised 89 to 99 percent of stomach contents, the remaining material consisting almost exclusively of insect and other invertebrate remains. Within the samples collected in grasslands ( $N = 29$ ), rain forest ( $N = 13$ ), and on Majuro atoll ( $N = 4$ ), there was considerable variation in the amounts of vegetable and animal matter present, with those collected in the rain forest having the highest percentage of animal matter (11 percent). Baker (1946), working on Guam, estimated that plant remains totalled 80 percent of stomach contents, the remainder consisted of insects and other invertebrates. Harrison (1954) found similar proportions of plant to invertebrate material in the stomachs of *R. exulans* in Malaya and, in addition, noted that about 50 percent of the diet of two subspecies of *R. rattus* consisted of insects.

Despite the apparently low animal protein intake by *R. exulans*, this rat appears unable to survive satisfactorily on vegetable diets alone. Caum (1922) showed that rats fed only on sugarcane exhibited symptoms of malnutrition and partial starvation. Strecker and Jackson (1962a) demonstrated that rats fed on pure coconut lost weight.

Doty (1945) considered the availability of

proteinaceous foods to be a factor limiting populations of rats (*R. exulans* and *R. rattus*) in cane fields and adjacent waste areas. This seems doubtful in view of the high proportion (31.4 percent) of insects and insect eggs in the diet of *Mus musculus* when this mouse occupies the same habitat as *R. exulans* (Kami, 1966). There is a question, however, of unit effort involved. Although it may be economical for an animal the size of *Mus musculus* (average weight 12 g) to feed extensively on small insect eggs or larvae, it may not be so for one the size of *Rattus exulans* (average weight 55 g). These two species presumably will occupy slightly different niches within the cane field environment, but this factor alone does not necessarily account for the marked differences in their dietary compositions. The proportion of insects and other invertebrate matter in the diet of *Mus musculus* suggests that there is no shortage of proteinaceous material in the cane fields but does leave unanswered the problem of foraging effort. It is conceivable that the apparently large differences in the amount of animal protein eaten by *Mus musculus* and *Rattus exulans* are an indicator of the lower protein requirements of *R. exulans*, for a similar situation was found to exist between *R. rattus* and *R. exulans* on Eniwetok (Fall et al., 1971). Insect parts occurred in 33 percent of the stomachs of *R. rattus* and in less than 10 percent of those of *R. exulans*, this despite the fact that habitats occupied by these two species appeared to contain similar insect populations. Clearly the impact of foraging effort would not apply in this latter case.

The importance of animal protein in the diet of rats cannot be determined without greater knowledge of the protein content of vegetation used as food. In addition, making an accurate assessment of insect or other animal matter intake (quantity and quality) by rats is difficult. Rudge (1968), working with the common shrew, *Sorex araneus*, found that fragmentation of insect prey, unequal digestion time, and rapidity of passage through the gut made quantitative analysis very difficult. Such problems apply, though to a lesser extent, to the analyses of rat gut contents, at least in relation to insect and other animal matter.

## REPRODUCTION

Most information on *Rattus exulans* reproduction has been reviewed by Jackson (1962) in association with studies on Ponape. Since then Egoscue (1970) has presented additional information derived from a laboratory colony based on animals collected on Eniwetok atoll, Marshall Islands, early in 1962.

Litter size was found to range from one to 10 (average 3.8) and efforts to increase this figure by selection were unsuccessful. One to 13 (average 5.2) litters were born each year with most females having a reproductive lifespan of less than 1 year. The minimum nonlactating gestation was 23 days, with lactation prolonging gestation 3 to 7 days.

Despite the researchers' lack of success in selecting for larger litters, the laboratory colony had a higher average (3.8) than any of the field populations investigated in the Caroline and Marshall islands where the average was 2.5 on Ponape ( $N = 203$ ) and 3.0 on Majuro ( $N = 68$ ). Nevertheless, the laboratory average was below that recorded by Harrison (1951) in Malaya (average 4.5,  $N = 38$ ). Jackson (1965) considered that, because the Malayan populations have higher probabilities of dying (possibly because of higher levels of predation), such elevated reproduction rates are not unexpected and do not detract from the rest of his data which support the general thesis that a longitudinal correlate to reproduction in certain mammalian groups exists. Certainly Jackson presents litter size data from seven sites ranging from 5 to 40 degrees of latitude which show a positive regression of litter size with latitude.

## DENSITIES

Assessing population numbers of small rodents, including *R. exulans*, has proved difficult in many parts of the world. There are few good population estimates for *R. exulans* in any part of its range.

Baker (1946) obtained estimates for a 3.2-acre plot of coconut plantation on Guam and found that numbers ranged from 2.5 per acre in May to 8.4 in October. Strecker (1962) applied a modification of the Lincoln index (after Hayne,

1949) to capture-recapture data from a grassland and coconut area on Ponape. The former had densities ranging from 18 per acre in May to 30 per acre in October, while the latter ranged from 26 per acre in November to 59 per acre in June.

Several estimates of the numbers of *R. exulans* in the Tokelau Islands were made during 1966 and 1967 (Wodzicki, 1967) using capture-recapture techniques. Estimates ranged from  $17 \pm 1$  to  $74 \pm 8$  per acre in coconut groves. However these estimates were derived from very small grids and it is unlikely that the assumptions underlying the estimates were met.

In Hawaii (Tomich, 1970) the number of *R. exulans* occupying a dry gulch area was found to fluctuate from one to 13 per acre during the course of a 4-year study, with a marked peak occurring each year in early winter.

With one exception (Wodzicki, 1967), already discussed, all population estimates of *R. exulans* published to date have not included confidence limits and, in most cases, it is unlikely that the basic assumptions of estimation methods were met. The most important of these assumptions are that the population is static (i.e., no births, deaths, immigrations, or emigrations) and that there is uniform probability of capture for all animals. Only methods (i.e., Jolly, 1965) of analyzing capture-recapture data which take into account these factors can provide estimates with any degree of accuracy and even then they are critically dependent on field techniques.

## MOVEMENT AND HOME RANGE

All home range studies, with the exception of Tomich's study (1970), were reviewed by Jackson and Strecker (1962) when they were considering the results of their studies on Ponape; therefore, only a brief outline will be included here.

Areal home range estimates can be calculated in a variety of ways but most are subject to the criticism that the animals may move over runways rather than wander generally over the area. It is, therefore, more meaningful to consider linear distances between successive captures rather than the distances moved from point of original capture (Jackson and Strecker,

1962). Thus on Ponape 70 percent of the successive recaptures of *R. exulans* were within 60 ft of each other. On Guam, Baker (1946) obtained similar figures (77 percent within 75 ft). In Hawaiian cane fields and adjacent gulches, Kartman and Lonergeran (1955) found that 85 percent of the recaptures of *R. exulans* were within 50 ft of the original point of capture. In contrast, Spencer and Davis (1950), who worked on an overgrown Hawaiian mountain slope, found only 53 percent of the captures occurred within 100 ft of the point of original capture and 81 percent within 200 ft.

Harrison (1958), apparently being dissatisfied with existing methods of expressing home range, developed a new statistic, the standard range. It is expressed as the diameter of a circle within which 68 percent of the captures occur. *Rattus exulans* in Malaya was found to have a standard range of approximately 210 ft, which is almost twice that estimated for the Ponapean population. This is probably indicative of a lower population density in Malaya, for Jackson and Strecker (1962) found home ranges to be inversely related to population density (as measured by trap success) on Ponape.

Tomich (1970) provided a considerable amount of information on the movements of *R. exulans* in cane and adjacent gulch areas in Hawaii. Brant's (1962) method of analyzing movements was applied, this being the average distance between captures (avg D) over a short (4 days) or long (over 1 month) period of time.

The short term avg D for males was 82 ft and for females, 72 ft (no significant difference), whereas long term avg D were 113 ft and 91 ft, respectively (significant difference). These figures are averages for all habitats sampled—gulch, grass, field, and cane areas—but movement within the gulch was much more restricted than movement in cane or grassland areas. When computing home range, Tomich followed Stickel's (1954) use of linear measure, adjusted range length (A.R.L.). A.R.L. is the straight line distance between the most widely separated sites of capture for the individual rodent, with a correction factor of one-half the distance to the next nearest trap added to each end. The average A.R.L. for all habitats was found to be 228 ft for males and 214 ft for females.

Although the methods of expressing movement and home range outlined above all differ, it would appear that most individuals of *R. exulans* spend their lives in a relatively small area, the actual size being apparently dependent on the nature of the habitat. Shifts in home range and long range movements do not appear to be very common.

#### INTERSPECIFIC COMPETITION

A notable feature of the ecology of *R. exulans* is the apparent variation, within the geographic range, in the ability of this rat to associate with the other species. Thus, there is a complete gradation from close association with other species, as seen in Malaya, to apparent exclusion from a habitat, as seen in New Zealand.

The disappearance of *R. exulans* in the North Island of New Zealand occurred at the same time as *R. norvegicus* became common. It has been generally assumed that the latter "drove" out the former; in short, that competition occurred (Watson, 1957). For what the two species were competing is far from evident.

Searle and Dhaliwal (1957) investigated the distribution of four species of *Rattus* (*R. annandalei*, *R. exulans*, *R. norvegicus*, and two subspecies of *R. rattus*) on Singapore Island. The notable feature was the presence of so many species in an area that had been transformed from sparsely populated jungle to an urban environment in less than 150 years. With the exception of *R. norvegicus*, all species appeared to share similar habitats. *R. norvegicus* was confined primarily to the dock area and was not found more than one-half mile inland.

This distribution of *Rattus* species may provide a clue to the extinction of populations of *R. exulans* in some areas of New Zealand. *R. norvegicus* is considered to be a temperate species, in contrast with *R. exulans* which is primarily tropical and, as such, is probably physiologically better adapted to the New Zealand climate than is *R. exulans*. The reverse would seem to be the case in an area such as Singapore.

The role of macroclimates and microclimates has rarely been considered when discussing hypothetical competition among *Rattus* species in the Pacific area (Barbehenn and Strecker,

1962; Watson, 1957). Nevertheless, it seems reasonable to postulate that the initial exclusion of *R. exulans* by *R. norvegicus* on the North Island of New Zealand may have been due to the latter's physiological superiority in a colder climate. In other words, a temperate species (*R. norvegicus*) superseded a tropical one (*R. exulans*) at the limit of the latter's range. There are obviously many other factors involved, such as habitat diversity within an environment (discussed below) and available food supply.

The amount of competition between tropical *Rattus* species has not been well assessed. Harrison (1957) provided some evidence of habitat separation between species sharing a common vegetation type in Malaya. Evidence is based on the difference in infestation by trombiculid mites. Large numbers of one species of mite (*Trombicula akamusbi*) were found on two subspecies of *R. rattus* but comparatively few were found on *R. exulans* and *R. whiteheadi* who occupied the same macrohabitat. Similarly, individuals of *R. exulans* and *R. whiteheadi* were found to be parasitized predominantly by the same mite (*Walchia lewthwaiti*), a species which was absent from *R. rattus*. Inasmuch as the predominant mite found on *R. rattus* occurred primarily on the surface of the ground, it would appear that *R. exulans* and *R. whiteheadi* do not often come in contact with the surface of the ground. It is unlikely that host specificity accounts for this mite distribution, for the species involved are freeliving and the larval stages parasitize any mammal or bird that comes their way (Hughes, 1959). Here then is an example of three species living close together, yet apparently maintaining a degree of ecological separation and thereby reducing interspecific competition.

On Pacific islands is found also a vertical separation of species, particularly on coconut plantations (Baker, 1946; Barbehenn and Strecker, 1962; Burrows and Spiro, 1953; Heyerdahl, 1940). Individuals of *R. rattus* appear to occupy the palm crowns at night, possibly to forage for insects as well as occasionally to attack immature coconuts. *R. exulans* is diurnal and *R. rattus* tends to be exclusively nocturnal; this difference enhances separation of the two species, even under conditions when both species are confined to the ground.

That *R. exulans* and *R. rattus* can live together in a small area was adequately demonstrated by Strecker and Jackson (1962*b*). They confined several rats of each species in a small enclosure (10 ft × 10 ft) for 14 days; they then trapped all rats, examined them for signs of conflict, and noted any weight losses. The results indicated that, when food and separate niches were available, the two species can live satisfactorily in a confined space. However, recent work by Barnett (1964) adds a complication. He found that, if males of *R. rattus* and *R. norvegicus* were added simultaneously to an enclosure, they lived together without conflict. The situation was changed if the males were introduced at 10-minute intervals. This brief period evidently allowed the firstcomers to establish territorial rights within the cage which they defended against later entrants. In three such colonies studied, fighting and a high death rate occurred. Would this latter result also have occurred in colonies of *R. exulans* and *R. rattus* under the same conditions? If so, it would suggest that spatial separation may be essential for the survival of the species living together.

#### OTHER ASPECTS OF POPULATIONS

Aspects such as growth and development, longevity and mortality, and sex ratios have been fully reviewed by Jackson and Barbehenn (1962) in association with studies on Ponape and there is little point in reiterating them here. As far as I am aware, the only work subsequent to that review is that of Wodzicki (1967) and Tomich (1970).

#### LITERATURE CITED

- AUDY, J. R., and J. R. HARRISON. 1951. A review of investigations on mite typhus in Burma and Malaya. *Trans. R. Trop. Med. Hyg.* 44: 372-404.
- BAKER, R. H. 1946. A study of rodent populations on Guam, Mariana Islands. *Ecol. Monogr.* 16: 393-408.
- BARBEHENN, K. R., and R. L. STRECKER. 1962. Intra- and interspecific behavior: Field data, p. 166-173. *In*: T. I. Storer [ed.] *Pacific island rat ecology*. Bull. Bishop Mus., Honolulu 225. 274 p.

- BARNETT, S. A. 1964. Social Stress, p. 170-211. *In*: J. D. Carthy and C. L. Duddington [ed.] Viewpoints in biology. Vol. 3. Plenum Publ. Corp., New York.
- BIANCHI, F. A. 1961. Rat populations of the Hawaiian sugar cane fields. Abstr. Symp. Pap. 10th Pacif. Sci. Congr., Honolulu. Bishop Mus. Press, Honolulu. 478 p.
- BRANT, D. H. 1962. Measures of the movements and population densities of small rodents. Univ. Calif. Publ. Zool. 62: 105-184.
- BUCK, P. 1949. The coming of the Maori. Whitcombe and Tombs, Wellington.
- BULLER, W. L. 1893. Note on the *Mus maorium* (Hutton). Trans. N.Z. Inst. 25: 49-50.
- BURROWS, E. G., and M. E. SPIRO. 1953. An atoll culture; ethnology of Ifaluk in the central Carolines. Hum. Relat. Area File, New Haven. iii+355 p.
- CAUM, E. L. 1922. Why do rats eat sugar cane? Hawaii. Plant. Rec. 26: 213-215.
- DARWIN, C. 1845. Journal of researches into the natural history and geology of countries visited during the voyage of H.M.S. *Beagle* round the world. J. Murray, London.
- DIXON, W. A. 1878. Notes on the meteorology and natural history of a guana island. J. Proc. Roy. Soc. N.S.W. 11: 165-175.
- DOTY, R. E. 1945. Rat control on Hawaiian sugar cane plantations. Hawaii. Plant. Rec. 49: 71-293.
- EGOSCUE, H. J. 1970. A laboratory colony of the polynesian rat *Rattus exulans*. J. Mammal. 5: 261-266.
- ELBEL, R. E., and M. THAINEUA. 1957. A flea and rodent control program for plague prevention in Thailand. Amer. J. Trop. Med. Hyg. 6: 280-293.
- ELLERMAN, J. R. 1947. Notes on some Asiatic rodents in the British Museum. Proc. Zool. Soc. Lond. 117: 259-271.
- FALL, M. W., A. B. MEDINA, and W. B. JACKSON. 1971. Feeding patterns of *Rattus rattus* and *Rattus exulans* on Eniwetok Atoll, Marshall Islands. J. Mammal. 52: 69-76.
- GRAY, J. E. 1843. Fauna of New Zealand. *In*: Dieffenbach travels in New Zealand. J. Murray, London.
- HARRISON, J. L. 1951. Reproduction in rats of the subgenus *Rattus*. Proc. Zool. Soc. Lond. 121: 673-694.
- . 1954. The natural food of some rats and other mammals. Bull. Raffles Mus. 25: 157-165.
- . 1957. Habitat of some Malayan rats. Proc. Zool. Soc. Lond. 128: 1-21.
- . 1958. Range of movement of some Malayan rats. J. Mammal. 39: 190-206.
- HAYNE, D. W. 1949. Two methods for estimating population from trapping records. J. Mammal. 30: 399-411.
- HEYERDAHL, T. 1940. Marquesas Islands. Proc. 6th Pac. Sci. Congr. 4: 543-546.
- HOWLAND, L. 1955. Howland Island, its birds and rats, as observed by a certain Mr. Stetson in 1854. Pacif. Sci. 9: 95-106.
- HUGHES, T. E. 1959. Mites or the Acari. Athlone Press, Univ. Lond., Great Britain.
- HUTTON, F. W. 1877. Note on the Maori rat. Trans. N.Z. Inst. 9: 384.
- . 1887. Note on the rat that invaded Picton in March 1884. Trans. N.Z. Inst. 20: 43.
- IVENS, W. G. 1927. Melanesians of the southeast Solomon Islands. K. Paul, Trench, Treubner, and Co., London. xix+529 p.
- JACKSON, W. B. 1962. Reproduction, p. 92-107. *In*: T. I. Storer [ed.] Pacific islands rat ecology. Bull. Bishop Mus., Honolulu 225. 274 p.
- . 1965. Litter size in relation to latitude in two murid rodents. Amer. Midl. Nat. 73: 245-247.
- JACKSON, W. B.; and K. R. BARBEHENN. 1962. Population studies: growth and development, p. 80-89. *In*: T. I. Storer [ed.] Pacific island rat ecology. Bull. Bishop Mus., Honolulu 225. 274 p.
- JACKSON, W. B., and R. L. STRECKER. 1962. Ecological distribution and relative numbers, p. 45-63. *In*: T. I. Storer [ed.] Pacific island rat ecology. Bull. Bishop Mus., Honolulu 225. 274 p.
- JOHNSON, D. H. 1962. Rodents and other Micronesian mammals collected, p. 21-38. *In*: T. I. Storer [ed.] Pacific island rat ecology. Bull. Bishop Mus., Honolulu 225. 274 p.
- JOLLY, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration—stochastic model. Biometrika 52: 225-247.
- KAMI, H. T. 1966. Foods of rodents in the Hamakua district, Hawaii. Pacif. Sci. 20: 367-373.

- KARTMAN, L., and R. P. LONERGAN. 1955. Observations on rats in an enzootic plague region of Hawaii. Publ. Hlth. Rep., Wash. 70: 585-593.
- KING, J. E. 1955. Annotated list of birds observed on Christmas Island, October to December 1953. Pacif. Sci. 9: 42-48.
- MARPLES, R. R. 1955. *Rattus exulans* in Western Samoa. Pacif. Sci. 9: 171-176.
- MARTIN, J. 1827. An account of the natives of the Tongan Islands, in the South Pacific Ocean, with an original grammar and vocabulary of their language. Compiled and arranged from the extensive communications of Mr. William Mariner, several years resident in those islands. 3rd ed. Printed for Constable and Co., Edinburgh. 2 vols.
- MEESON, J. 1884. The plague of rats in Nelson. Trans. N.Z. Inst. 17: 199-207.
- NICHOLSON, A. J., and D. W. WARNER. 1953. The rodents of New Caledonia. J. Mammal. 34: 168-179.
- PEALE, T. R. 1848. Mammalia and Ornithology, p. 47. In: United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N. Vol. 8.
- RUDGE, M. R. 1968. The food of the common shrew *Sorex araneus* (Insectivora: Soricidae) in Britain. J. Anim. Ecol. 37: 565-581.
- SEARLE, A. G., and S. S. DHALIWAL. 1957. The rats of Singapore Island. Proc. 9th Pacif. Sci. Congr. 19: 12-14.
- SMITH, F. J. 1969. Rodent research in the Gilbert and Ellice Islands Colony, 1967-1969. Publ. Dep. Agric. Gilbert and Ellice Islands Colony.
- SPENCER, H. J., and D. E. DAVIS. 1950. Movements and survival of rats in Hawaii. J. Mammal. 31: 154-157.
- STAIR, J. B. 1897. Old Samoa or flotsam and jetsam from the Pacific Ocean, p. 296. Religious Tract Society, London.
- STEAD, E. F. 1936. The Maori rat. Trans. Roy. Soc. N.Z. 66: 178-181.
- STICKEL, L. F. 1954. A comparison of certain methods of measuring ranges of small mammals. J. Mammal. 35: 1-15.
- STONE, W. 1917. The Hawaiian rat. Occ. Pap. Bishop Mus. 3(4): 251.
- STRECKER, R. L. 1962. Population levels, p. 74-79. In: T. I. Storer [ed.] Pacific island rat ecology. Bull. Bishop Mus., Honolulu 225. 274 p.
- STRECKER, R. L., and W. B. JACKSON. 1962a. Habitats and habits, p. 64-72. In: T. I. Storer [ed.] Pacific island rat ecology. Bull. Bishop Mus., Honolulu 225. 274 p.
- . 1962b. Intra- and Interspecific behavior: data from captive rats, p. 173-176. In: T. I. Storer [ed.] Pacific island rat ecology. Bull. Bishop Mus., Honolulu 225. 274 p.
- TATE, G. H. H. 1935. Rodents of the genera *Rattus* and *Mus* from the Pacific islands. Bull. Amer. Mus. Nat. Hist. 63: 145-178.
- THOMSON, B. M. 1922. The naturalization of animals and plants in New Zealand. Canterbury Univ. Press.
- TOKUDA, M. 1933. On some rats and mice from South Sea Islands. Part I, *Rattus concolor* group. Annot. zool. jap. 14: 79-87.
- TOMICH, P. Q. 1969. Mammals in Hawaii: a synopsis and notational bibliography. Spec. Publ. Bishop Mus. 57. 238 p.
- . 1970. Movement patterns of field rodents in Hawaii. Pacif. Sci. 24: 195-234.
- WATSON, J. S. 1956. The present distribution of *Rattus exulans* (Peale) in New Zealand. N.Z. J. Sci. Tech., B, 37: 560.
- . 1957. Rats in New Zealand: a problem of interspecific competition. Proc. 9th Pacif. Sci. Congr. 9: 15-17.
- WODZICKI, K. A. 1950. Introduced mammals of New Zealand. Bull. N.Z. Dep. Sci. Industr. Res. 98: 88-101.
- . 1967. An ecological survey of rats and other vertebrates of the Tokelau Islands. Publ. Tokelau Islands Admin.
- WOODFORD, C. M. 1895. The Gilbert Islands. Geogr. J. 6: 325-350.