

Productivity in High and Low Islands with Special Emphasis to Rodent Populations¹

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Pacific islands of two principal types offer somewhat contrasting environments. The high island offers an environment of high annual rainfall (often in excess of 200 inches), moderate temperatures, and lush vegetation. The atoll is somewhat drier (usually less than 150 inches) and warmer (80°F. or higher average temperature), the more xeric conditions resulting in somewhat lower bioproductivity. (While my comments relate to experience in Micronesia and more specifically in the Marshalls and eastern Carolines, the parameters considered here relate to other areas of the Pacific as well.)

Island ecosystems are characterized (Fosberg, 1963) by limited resources and diversity, and a tendency for climatic equability. Wiens (1962) found that islands of less than 3.5 acres had but ten plant species; the floral diversity on larger islands was proportional to the area. He suggested that three and a half acres might be the minimum size for the development of a stable fresh water lens, a necessary requirement for most land plants. Species diversity also is affected by such factors as distance from other islands and major land masses (inversely as the square of the distance), air and water circulation patterns, migrational routes of birds (who may bring eggs, seeds or spores on their feet), rainfall (*e.g.*, with 19 inches of rain Canton has 14 plant species; Arno with 160 inches, 125 species).

Island populations are protected from outside competition and thus are subject to lower levels of interspecific competition than on continental areas, but once exposed to new forms may show extreme vulnerability. Mayr (1965) has examined this problem and concluded that the percent of endemic bird species on an island increases with the island's size at a double logarithmic rate; on small islands the rate of extinction is very high. In forms which have long evolved in isolation, narrow ecological delimitation occurs, making them especially susceptible to extinction when exposed to broadly adapted immigrants.

As part of this pattern, "ecological boiling" may occur when a form successfully survives the "distribution sweepstakes" and arrives in an ecologically open environment. Zimmerman (1961) suggested for the Hawaiian Islands such a fortuitous colonization every 20,000-30,000 years but indicated that 300-500 species might evolve from a single form. Only about 275 ancestral stocks produced the entire endemic flora of 2,000 higher plants.

Island ecosystem species of their very nature are very easily upset, resulting in a marked decrease in entropy. Man has had a profound effect on the islands he has subjugated. The successional pattern is stopped and often pushed back to an early stage. In terms of food production this may be very desirable;

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in terms of achieving a climax community with stability and self-perpetuation, many trophic layers, and lower primary production/unit biomass, this is disruptive.

But man is not the only disruptive element in this environment. Tropical storms have a great impact and can very quickly overturn the entire ecosystem, especially on an atoll. In the 1954 typhoon that hit Jaluit, lagoon sediments washed over the island, one-fourth of the island's soil was sluiced off, and up to 90% of the trees were destroyed. At least a decade was estimated as required for a marked degree of recovery (Wiens, 1962).

Pacific weather data indicate eighteen tropical storms (≥ 64 knots) north of the equator each year, but most are not near land (Blumenstock, 1961). Old men at Ifalik, for example, remembered only six in a lifetime (Bates, 1958). An island may pass half a century without a typhoon and then have two strike within a month. Patterns are highly variable over much of Micronesia.

Despite the savage attack of such storms, life does survive. Roots and tubers sprout; seeds protected from the salt water germinate; flies, mosquitoes, and spiders emerge from protected crevices; crabs and lizards somehow have found sufficient protection. Soil and leaf feeding insects suffer more. While rat numbers may be decimated, a nucleus often seems to survive; calculations indicate that complete repopulation can occur within a few years (French, 1966). Burrows or nest cavities apparently are not completely flooded, air pockets remaining—a situation not unlike that faced by hibernating ground squirrels subjected to early spring floods (Quanstrom, 1966). Climate-related catastrophes are not unknown to rats elsewhere (Davis, 1956).

On a high island, the land is not completely washed over by the ocean, but environmental disruption by typhoons is great. Some nests or young are destroyed by flooding. Vegetative cover may be sufficiently broken to alter the behavior and even the population dynamics of such animals as rats (Jackson, 1962).

Biomass and productivity data for tropical islands seem largely lacking. Studies such as that of Golley (1960) in an old field community or even the synthesis of data from continental forests by Ovington (1965) seem not to be available for tropical islands. Virtually all published observations have been qualitative in nature; nothing comparable to the coral reef study by the Odums (1955) has been done for terrestrial communities, although both the study of Marcus Island (Sakagami, 1961) and the diverse reports of the Pacific Science Board projects, when drawn together, provide partial exceptions.

Our plant data for a northern Marshalls atoll (Eniwetok) and for Ponape, a high island, show a total basal area of about 500 ft²/ha in both environments for undisturbed forest areas, though there are fewer individuals per unit area in the high island forest than in the atoll *Pisonia* grove (Table I). Observations by Hatheway (1955) on Canton give higher density figures but basal area values seem to fall into place. Densities of less than 500 trees per hectare in continental tropical forests (Richards, 1957) are less than one-half those found in island stands. Continental forests are composed of more than 70 species while Micronesian forests have at best several dozen, often on atolls less than half a dozen.

Productivity data are even harder to find. Ovington (1965) summarizes much of the available data; newly available data expand the scope somewhat (Table 2).

Table 1. Characteristics of Tropical Forests

	Ref.	No. Species	No. Trees/ha	Basal Area (ft ² /ha)
<i>Atoll</i>				
N. Marshall Islands* (Eniwetok-Igurin)	1	4	2100 (1159**)	480
(Eniwetok-Muti)		4	1533 (833**)	400
Canton Island***	2	<i>Cordia</i>	6900	670
		<i>Messerschmidia</i>	2870	327
<i>High Island</i>				
E. Carolines* (Ponape)	3	6	1800	508
Mauritius**	4	52	1710	
<i>Continental</i>				
Ivory Coast**	4	74	530	
Nigeria**	4	70	390	
British Guiana**	4	91	432	
Coconut Plantation		1	148	

* $\geq 1''$ DBH** $\geq 4''$ DBH*** $\geq 2''$ DBH

References:

1. Jackson, unpublished
2. Hatheway, 1955
3. Jackson and Strecker, 1962
4. Richards, 1957

Table 2. Plant Biomass Characteristics of Tropical Areas

Plant Community	Ref.	Total Biomass (kg/ha, dry wt)	Annual net Primary Prod. (kg/ha, dry wt)
Mixed tropical forest	1	255,900 (Maximum 500,000)	33,000
18 yr. evergreen forest (Ghana)	1	154,000	10,000
Rain forest (Indonesia)	2	127,900-292,500*	5,800
Rain forest (Thailand)	4		11,200
Montane forest (Indonesia)	2	549,234*	12,400
Montane grassland (<i>Miscanthus</i> , Japan)	3		6,000
Meadows	1		12,000
Grass swamp	1		77,000
Sugar cane (@ 10 T/A)			11,221**

* Stem biomass only

** Wet weight

References:

1. Ovington, 1965
2. Soerianegara, 1966
3. Iwaki, et al., 1966
4. Kira and Shidei, 1966

Maximum total plant biomass in the tropical forest was estimated by Ovington to exceed 500,000 kg/ha, and this prediction was fulfilled; see Table 2.

Because productivity in agricultural crops is usually given in wet weight ratios (or at best as fire dried, as with copra) and foresters use oven dry weights, comparisons of productivity are difficult. Annual net primary production in grassland and meadow areas (10-12,000 kg/ha, dry wt.) is not greatly different from that calculated for sugar cane fields (11,000 kg/ha, wet weight) if the biennial harvest (ave.=10 T/A) is divided between the two years.

These kinds of data are lacking for the small islands of Micronesia and Polynesia. At best, some agricultural data can be cited. Annual copra production (based on 60 trees/A) could be in excess of 1200 kg/ha, (fire dried wt.) but density and productivity are highly variable; see, for example, Alkire, 1965 (p. 78). Breadfruit production might exceed 5000 kg/ha (wet weight). But of course the fruits or seeds represent only a portion of the annual primary production of a plant community.

In terms of animals, our principal concern is with rodents and in particular with the two species most widely distributed across the Pacific islands, the Polynesian rat (*Rattus exulans*) and the roof rat (*Rattus rattus*) (Fig. 1). The Polynesian rat probably arrived in the same outriggers as did the first Polynesians and Micronesians; the roof rat arrived somewhat later in trading ships from the Philippines, Japan, and other countries of both West and East, depending on the specific island in discussion. In some cases great mixing of subspecific forms has occurred. Two other rodent species, the Norway tra (*Rattus norvegicus*) and the



Fig. 1. Roof rat (*Rattus rattus*) caught in live trap. This rat was marked by toe clipping and released as part of a study of movement patterns and longevity (Runit island, Eniwetok Atoll)

Table 3. Summary of Densities of Rat Population in Various Island Habitats

Roof Rat (<i>Rattus rattus</i>)	Ref.	Specific Habitat	Rats/ 100,000 ft ²	Method of Determination
<i>High Island</i>				
E. Carolines (Ponape)	1	tall grassland formation	3.7	3-day removal trapping
		coconut plantation	7.9	"
		mountain rain forest	3.7	"
Guam	2	grassland	23.0	removal trapping
		forest	11.5	"
Cryperus	3	grassland-woodland	23.0	live trapping
		4	carob plantation	2.3-4.6
<i>Atoll</i>				
Marshalls (Majuro)	1	coconut plantation	10.5	4-day removal trapping
Marshalls (Eniwetok)	5	short grassland (40% ground cover)	18.5	all animals live trapped in 4-6 week period
<i>Rattus conatus</i>				
Australia (Queensland)	6	sugar cane	71.2	estimates from live trap grids
<i>Polynesian Rat (Rattus exulans)</i>				
<i>High Island</i>				
E. Carolines (Ponape)	1	tall grassland	24.1	3-day removal trapping
		coconut plantation	43.0	"
		mountain rain forest	21.5	"
Guam	2	grassland	18.4	removal trapping
		forest	13.8	"
	3	grassland-woodland	18.4	live trapping
<i>Atoll</i>				
Marshalls (Majuro)	7	coconut plantation	48.0	4-day removal trapping
Marshalls (Eniwetok)	5	coconut plantation	40.0	all animals live trapped in 4-6 week period

References:

1. Strecker, 1962
2. Barbehenn, 1966
3. Baker, 1946
4. Watson, 1952
5. Jackson, unpublished
6. McDougall, 1946
7. Jackson and Strecker, 1962

house mouse (*Mus musculus*), are also found, usually in small populations, especially on the high islands. Since they do not usually thrive in a feral condition isolated from human activity (some important exceptions to this generalization occur, as in Hawaii), they will not be considered at length here.

Productivity data for rat populations are even more limited. The best we can do is to cite population densities in various island habitats (Table 3) which

are given as rats/100,000 ft², or approximately a hectare. Polynesian rats showed densities of 40-50 animals/ha in coconut plantations, about half that in grasslands and forests. Roof rats were sparse (<10/ha) on the high island of Ponape, somewhat more abundant (10-23/ha) on Guam and in corresponding atoll situations. A difference in body size (75 gm vs. 150 gm) is hardly proportional to the difference. Since food habits are very similar, another mechanism, perhaps behavioral, is needed to explain the consistently higher density of Polynesian rats. A similar form in Australia (*R. conatus*) exists in cane fields at a mean density in excess of 70/ha (McDougall, 1946).

In contrast, interspecific competition on an island may be of low intensity or be limited to very narrow areas of niche overlap. Indeed, among the vertebrates there is little in the way of a predator-prey relationship. Rats are almost entirely vegetarian, and on most islands have no predators of consequence. Birds and reptiles are often in a like position. The lack of interspecific competition is another measure of the depauperate fauna on these islands, a result, as with plants, of the isolating effect of the ocean.

Intraspecific competition in island populations may be very intense. This characteristic has profound effects on the population dynamics of the species. Our data on rats suggest very stable populations with low reproductive rates, long life span, and high survival—all in direct contrast to rat populations elsewhere in the world. To further emphasize the aspect of lowered reproductive rates, a direct correlation between latitude and litter size has been demonstrated (Jackson, 1965).

Allee & Schmidt (1951, p. 631), in discussing insular faunae, indicate that dwarfing of birds and mammals in such environments is correlated with the limitation of space. No tendency toward dwarfing has been found in our studies of Micronesian rats, and we have also failed to find such a tendency in data from Hawaii and other areas of Polynesia and Micronesia.

Rats, of course, are not the only mammals introduced onto various islands in recent times: the carabao from Asia, the deer from Japan and Europe, the dog and pig from the West are further examples. Special breeds of cattle are being developed for high island conditions; goats are present in limited numbers but usually are not feral. Horses have been introduced, usually unsuccessfully.

Rabbits, the plague of Australia and some areas of Japan, have never been successfully introduced—or even attempted—to my knowledge in Micronesia. Early introductions onto small islands in the Hawaiian chain (e.g., Laysan) were eminently successful (Tomich ms.); the ecosystems there have been severely disrupted and are unlikely to recover until the animals are removed. Successful introductions in several other Polynesian islands have occurred (Watson, 1961).

When I was on Ponape the district administrator wished to introduce rabbits to augment the protein supply available to the island population. This introduction I vigorously opposed because of the history of such introductions elsewhere, but I have often wondered what actually might have happened. The observations of Howard (1957) in Australia indicated that rabbits in areas of tall grass did poorly because the fur was so readily wet by rain and dews. Certainly the prime available habitat on Ponape was large areas of tall dense *Ischaemum* grass; perhaps hutch escapees would not have been able to establish themselves, but the



Fig. 2. Damage to green coconuts by roof rats. The center nut in the upper row was opened and used for a drinking nut and is showed for comparison (Majuro)

test was never made.

Certainly introductions of the marine toad (*Bufo marinus*) and the African snail (*Achatina*) have created problems; in like manner insect and plant (weed) introductions have caused many complications, but these non-mammalian topics have provided grist for other symposia.

Like plant weeds, the introduced animals often have disrupted the ecosystem severely. Rats, for example, have made the growing of many cultivated crops difficult and expensive, if not impossible, on many islands. As in other parts of the world, the intensity of pest problems is correlated with the tendency toward monospecific agriculture.

Copra, the cash crop of most islands, often may be produced only when trees are protected by banding or by using chemical control measures. In virtually all islands only the roof rat is involved in coconut depredations (Fig. 2). (Interestingly on some high islands the roof rats do not invade the coconut trees; this perhaps is related to subspecific differences among rats.) In similar ways cacao (Fig. 3), vegetable crops, cane (Fig. 4), and rice are affected.

In order to produce sufficient food for the human population and the islands' export needs, control of pest species is necessary. While it is easy to suggest that environmental and biological control methods are the best, implementation is often more difficult. The mongoose and monitor lizard as rat predators have failed whenever introduced and often have done incalculable damage to the ecosystem. Cleaning up the environment by providing barrier strips and eliminating harborage may be workable, but often the rocky substrate of the high islands



Fig. 3. Damage to cacao pods by roof and Polynesian rats (Ponape)

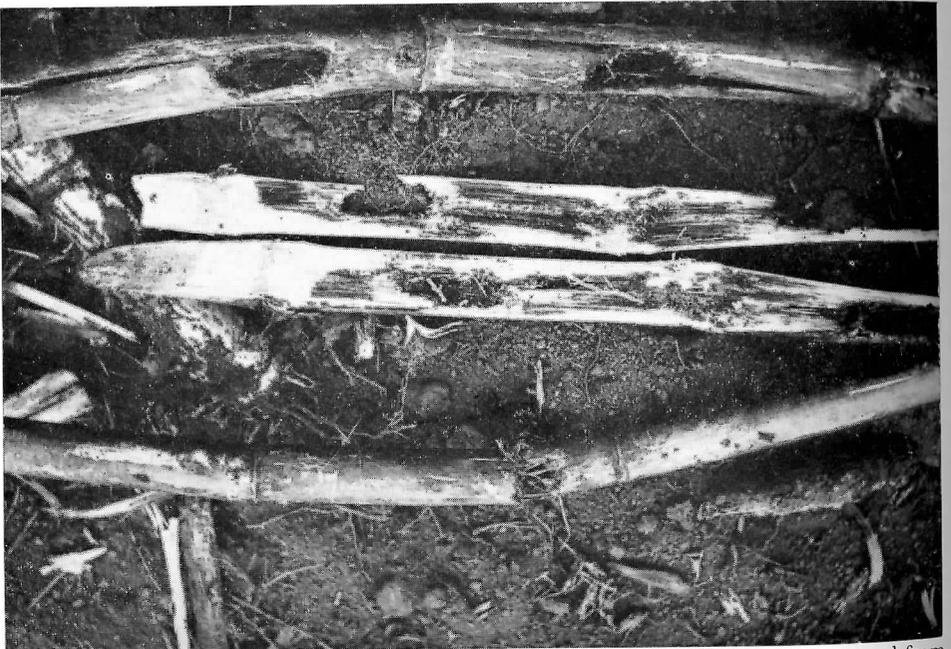


Fig. 4. Damage to sugar cane by rats, showing the internal fermentation which has spread from the site of feeding (Hawaii)

and the rapid rate of vegetation regrowth provide continuing nesting sites and sources of food.

When useable environmental controls are inadequate, chemicals are often resorted to. The use of toxicants for rodent control (at least outside of Hawaii and the Philippines) has been restricted largely to anti-coagulants. Their chronic nature makes them safe to use close to human habitations and where domestic animals might accidentally ingest them. Recent development of chemosterilants and the acute rodenticide, Raticate, which is specific to the genus *Rattus*, may offer additional tools if the price is low enough. In many areas the cost of these chemicals is such that unless the crop has high cash value (like cacao or garden vegetables) rat control with these materials is not economically possible without government subsidy.

In addition to the roles played by climate and by plant and animal introductions in disrupting the ecosystem, man has done much himself directly. Today the war scars are covered by maturing vegetation moving along a somewhat unsteady but inexorable route toward climax stability.

But what of the future? Can conservation—the prudent use of natural resources—become a way of life? Certainly the pre-war Japanese policy of island self-sufficiency in primary production is unlikely to be repeated. The Japanese agricultural practices were conservative; the Micronesian practices are not always so. The burning of hillsides during the dry season to clear the land is a pan-tropical (indeed world-wide) characteristic. The land is used several years before it reverts to the “boondocks,”* its fertility gone; erosion may be rampant. (Though it ought to be mentioned parenthetically that erosion and weathering are not “evil” processes; in areas of primitive soils perhaps they should be encouraged!)

The thin and often sandy soil, impoverished by leaching and growing nutritionally starved plants, can be dramatically improved with fertilizers. Significantly greater yields and earlier maturation of crop species result in the carrying capacity of the land being greatly increased and returning the cost of the treatment. While this is being done, public health officers have promoted the self-flushing benjo and pigpen built over tidal flats, carrying valuable fertility out to sea rather than returning it to the land.

Fishing on a commercial scale constitutes an important energy harvest and could support a significant increase in the carrying capacity. However, it should be noted that on some atolls the lagoon may be close to maximal exploitation (Wiens, 1962). But high islanders must be trained and encouraged to become fishermen; for many it is not an expected vocation.

Perhaps the most critical loss of resources is that of “brain drain.” Micronesians, to obtain the necessary technical and professional training, often must go to mainland areas or larger island centers. Reluctance to return and apply the new skills and ideas to local problems constitutes an increasing dilemma.

With limited or lacking mineral resources, with agriculture often best limited to tree crops, the development of a service industry—tourism—is a considered possibility. Problems of logistics and mores are not insignificant. For many of

* A term of Filipino origin meaning “secondary, weedy scrub vegetation”; much like the type denoted by the Malayan “belukar”.—Editor.

the less accessible areas of Micronesia, the development of the extensive sand beaches, the wonders of the coral reef, the bounty of the turquoise lagoon, and the game animals of the mountain will be an expensive operation and available only to the few willing to pay the price. But the development of exotic retreats and vacation sites is a coming specialty, though I suspect that many of us would prefer not to see this threat on the horizon and would wish for another approach to economic stability of the islands of Micronesia.

The world is in the age of industrialization and nuclear energy. The Pacific islands, willing or unwilling, are being dragged into this age. The problems of cultural shock, of changing mores, of necessary resource development, of population pressure all must be met, and all too often, unfortunately, these changes are mandated by government fiat rather than by generation from the governed (Taeuber, 1966). To best integrate the pressures of the world and the needs of the islands and their people is the modern dilemma.

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