CHAPTER 13

GENERAL DISCUSSION

This study has provided some new understanding on the population ecology of the feral pig and the pigs' inter-relationships with plant and animal communities in the island rain forest habitat in Kipahulu Valley. Three broad questions remain to be asked which cut across the subject areas discussed in the previous chapters:

1) Has the population erupted?

2) What factors limit this population?

3) How is it different from other populations?

Eruption is not always a rule among established ungulate or introduced populations, although this process can be expected of them (Riney 1964). In populations which show eruptions, three phases are often identifiable: (1) initial rapid increase in numbers to an eruptive peak, (2) decline, brought about by habitat modification and depletion of resource(s), and (3) oscillating fluctuations down to and about a low stable density (Caughley 1970, 1977).

Several habitat and mortality factors discussed earlier could act in combination to prevent eruption in this population. However, the evidence suggests that the potential to erupt was present in the invading feral population. Additionally, the Valley's rain forest was in a pristine state at the time of invasion by pigs, contained high densities of tree ferns and, thus, was capable of sustaining, at least temporarily, a large number of pigs.

Despite these factors, eruption, if it has indeed occurred in this population, is difficult to document without data for biomass of tree ferns and feral pigs through time. Analysis of natural history information from initial invasion at the mouth of the Valley until the present time, provided some meager evidence to suggest that the Kipahulu Valley population probably erupted sometime between 1967 and 1976, and possibly in the early 1970's.

Pig density in the interior of the Valley was low in 1967. Signs were limited to gently sloping terrain and the relatively undisturbed virgin forest "bear witness to the compatability of wild pigs and a wide variety of indigenous plant species" (Banko & Wilson 1967). Ten years later, in 1976, Lamoureux and Stemmermann revisited the Valley and reported "a great increase in the pig population" and a "considerable increase in amount of pig damage." In itself, the increase in numbers cannot be taken to infer a post-1967 eruption. This is because Caughley's eruption model is operationally defined. But the habitat in 1976 was described as "dramatically different." Feral pigs had modified and displaced the native habitat with exotics, principally the strawberry guava. The marked deterioration of the habitat was also evidenced by a more than 12-fold increase in open areas on the forest floor. The koa forest, described as pristine in 1969, no longer is, under the present evaluation. Impact on tree fern biomass is reflected by the paucity of tree fern regeneration. The size frequency distribution of tree ferns in the koa forest now consists of a peak representing individuals of older age classes between 13-30cm in trunk diameter and a smaller peak consisting of young plants less than 6cm in trunk diameter (Yoshinaga - unpubl. data).

The length of time between introduction and eruption differs among ungulates, and is shorter for smaller species (Caughley 1970). The wild boar in the Great Smokey Mountains National Park in Tennessee reached eruptive densities after an invasion history of 10 years and then fluctuated to a low stable density (Singer 1981). In Kipahulu Valley, eruptive densities were, by arguments in the preceding paragraphs, reached 20 years or approximately six generations after the onset of feralization. Why then was there a delay in eruption?

The apparent delay in the eruptive peak in the Kipahulu population may be attributed to terrain, the resulting restricted movement patterns and the relaxation of human predation on this pig population beginning in 1969 when the Valley became a natural reserve in NPS. Hunting during the early 1960's would be the most probable cause for the delay of an eruption. In some respects, the effect of hunting on population increase in the Valley's pigs may be analogous to the influence of disease, such as rinderpest, on African ungulates. Sinclair and Norton-Griffths (1979) observed that the elimination of this viral disease resulted in eruptions of native ungulates in the Serengeti plains. Thus, the reduction or removal of hunting would correspondingly remove the impedence to eruption.

Fundamentally, this study of the synecology of the feral pig in Kipahulu Valley focuses on the factors which could limit abundance or result in changes in the numbers of pigs. These factors may be broadly categorized into those that act: (1) on the younger age classes, (2) independently of age, and (3) on the older age classes. Food can be the single most important factor influencing numbers in animals by limiting productivity of young through protein limitation (White 1978) and adults through total caloric intake. This hypothesis raised at the outset of this study can now be discussed by considering the question: Were feral pigs limited by the quantity and quality of foods that were rich in energy and protein?

Feral pigs in Kipahulu Valley do not appear to be limted in numbers at the present time by the quantity of food. Their restricted movements and small home ranges are indicative of high food density in this habitat. Tree ferns, their staple, have high food volume and like all other herbaceous forage are available throughout the year. The strawberry guava provides another abundant staple during winter; a surplus of this food is indicated by unfed fruits during the season. Pigs dispersing the undamaged seeds of the strawberry guava in their home ranges have been increasing the availability of this food item in new areas at a later time. The wide dietary range suggests a reserve of potential foods, one or several of which could serve as a staple. The present dietary range includes many genera represented by several species. Since feeding was selective on plant parts high in nutritional content rather than on whole plant parts from particular species, the observed dietary range probably was comprised of about 60 plant foods, or 26.2% of the total plant species in the Valley. Not all of the remaining plant species (73.8%) would be foods, but the presently unimpacted plant populations contain several resources fed upon by other populations of pigs in Hawaii.

The availability of foods in quantity was also suggested by the presence of food in all stomach samples and the high proportion of full stomachs. No pig with signs characteristic of starvation, e.g., protusion of pelvic bones, was ever sighted in over 60 man months of field work.

Staple foods of pigs were exceptionally high in energy content. In strawberry guavas, total sugar constitutes about 10% dry matter (MacCaughley 1917). Tree ferns have the highest nitrogen free extract among all plant foods in the Valley and thus represent a primary source of energy. A mature tree fern contains in its core from 22 to 32kg pure starch (Neal 1965). Because of the high food volume and high energy content in tree fern core, it is very unlikely for a population subsisting on tree ferns to be limited by energy.

The data on proximate analyses in plant foods confirm White's (1978) assertion that protein is diluted in plants. However, the Valley pigs overcome this dilution by maximizing their intake of foods rich in nitrogen in three ways: (1) by feeding selectively on young plant parts and meristematic rather than structural tissues, (2) eating large volumes of foods as evidenced by the large stomach volume, and (3) supplementing their diet with animal protein.

The high importance value of earthworms in their diets (Chapter 6) and the great abundance of earthworms in these forest soils, further suggest that feral pigs are not limited by protein. The nutrient values in earthworms vary with species; in Lumbricine species, these values are 53 to 64% protein, 4 to 6% crude fat and 16 to 18% total carbohydrates (French et al. 1952). Earthworms thus provide essentially all the protein needs, energy from their crude fat and carbohydrate fractions and, additionally, calcium from calciferous species.

Chemical blood analyses support the argument that this rain forest population is not limited by nitrogenous foods. Levels of albumin, hemoglobin and BUN examined together, show that nitrogen intake and protein status are adequate. Thus, this population does not appear to be limited in abundance by the shortage of nitrogenous foods. What then are the factors limiting abundance?

Accidental mortality, entrapment in mud, inclement weather (rain, cold and high humidity) and inadequate rain shelters or farrowing nests are likely to be more important sources of mortality for newborn piglets and juveniles than for older animals. Mongoose predation may likewise contribute to population losses from below by removal of suckling pigs. There is some degree of overlap in the activity cycles of mongoose and feral pig in that the former is diurnal while the latter is crepuscular. Mongoose predation will become important whenever piglets are mud-entrapped, orphaned or separated from their mothers. Stray piglets are more vocal than when they are with their littermates and, hence, are more vulnerable to predation. Because of its relatively smaller size, there is an upper size limit beyond which the mongoose cannot effectively prey on pigs. Hence, mongoose predation is specific to the very young animals and its effect on the population is like a "piglet disease." The significance of mongoose predation to population mortality will be dependent on the relative densities of piglets and mongoose at any one time.

Parasites can be a direct source of mortality, or else increase the susceptibility of pigs to other mortality factors. High rainfall and wet soils are conducive for the maintenance of free-living stages in helminthic life cycles. Forest soils and invertebrates that served as secondary hosts are constant sources of parasite infection for the pigs. The availability of earthworms, the nematode-oligochaete paratenic association and the importance of earthworms in the diets of the pigs, collectively suggest that metastrongyllid and kidney worm infection will be maintained at a level of high prevalence in this population than the other helminths.

Failure of dentition (dento-alveolar diseases and tooth loss) was found to be the most serious disease of old age in the Valley pigs, and is considered a primary source of mortality in old animals. Food and habitat factors probably account for the severity in loss of tooth structure and individual teeth. Diets of pigs in this population are rich in sugars and fermentable carbohydrates. Foods became lodged in tooth cavities, interproximal spaces and bone pockets resulting in continuous availability of substrate to oral bacteria for acid production. The calcium and phosphorus content in pigs' teeth are 36.7% and 7.6%, respectively, on ash basis (Kicke et al. 1933). These minerals are lost from the teeth at pH below 5.5 (Sanders 1980). The very acidic forest soils with pH as low as 3.3 (Chapter 3) most probably assisted in decalcifying and eroding tooth structure, as was evidenced by the cup-like depressions in molars. Cupped teeth would be attrited faster than teeth with flat occlusal surfaces. The coarseness of the pigs' diet invariably influence teeth wear.

A number of features, many associated with the recency of feralization, distinguish this population from other feral populations which have been studied. Individuals had a higher frequency of lighter coat colors, relatively larger body size and pronounced domestic body conformations. These differences have been attributed to the late feral history and the improved European breed-types upon which this population was founded. While the lighter coats are likely to be maintained in this closed canopy forest population, the larger body size will probably not persist through continued feral existence in an undisturbed state because inbreeding tendencies, accentuated by topographic isolation and restricted movement patterns, will result in smaller-sized animals.

The most striking difference between this and other feral populations is its smaller home range. This can be explained by the high biological productivity in this non-seasonal, tropical rain forest habitat. In this environment, the maintenance needs (food, water and shelter) are concentrated, which reduces the need to range over a larger area. Food habits in this population are unique in that plant matter is derived almost exclusively from native plants, particularly tree ferns, and is a superior source of energy compared to energy foods used by pigs in other habitats. For instance, nitrogen free extract in tree ferns is higher than in acorns (NFE = 59 to 78% dry matter) (Barrett 1978), a key food in many wild and feral populations. Despite its good nutritional status, this population, unlike those contrasted, is characterized by neutrophilic leukocytosis, suggesting poorer health and a relatively shorter ecological longevity.