POPULATION BIOLOGY AND MANAGEMENT OF THE FERAL PIG (*SUS SCROFA* L.) IN KIPAHULU VALLEY, MAUI

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My wife, by some misfortune, has become associated with this study, and in performing functions as diverse as stomach content analysis, pick-up of specimens at the airport and delivery to various departments for analyses, data analyses and deciphering my drafts for a typeprint--duties quite alien to her professional training but which she almost always obliged. Finally, I wish to acknowledge Peggy Daniel, June Saito and the Cooperative Parks Resource Studies Unit for assistance in producing this final draft on the HP3000 Text and Document Processor.

ABSTRACT

The population ecology of the feral pig (Sus scrofa) was investigated in a topographically closed Hawaiian rain forest in Kipahulu Valley, Maui. This population, with a feral history of 35 years, probably erupted six generations after the onset of feralization. Emphasis was placed on investivating: (1) the factors which could limit abundance, and (2) population processes unique to this habitat. A natural history approach was used to examine the hypothesis that food quality, rather than quantity, could be limiting the population. Additionally, because of specific information needs of the National Park Service, particularly with regard to control programs, this study also sought to obtain management-related information as a basis for management recommendations.

Food habits were characterized by: (1) an omnivorous diet, consisting mostly of plant matter, (2) a staple of tree ferns, (3) a seasonal switch from tree ferns to strawberry guava, and (4) a strong reliance on earthworms as a source of animal protein. The dietary range covered 40 plant species; 62.5% were herbaceous species, 32.5% trees and a woody vine. Seventy percent of the forage were native plants of which 85.7% were endemics. Tree ferns were the most concentrated source of sugar and starch. Plant foods were low in protein, but feeding habits of the pigs resulted in maximization of foods rich in nitrogen. Blood profiles showed adequate nitrogen intake and protein status. Pig feeding habits resulted in the death of some native trees and damage to the ecosystem.

Feral pigs actively disperse the strawberry guava by transporting large quantities of seeds in their digestive tracts. Gut transport did not affect seed viability but hastened germination.

Home ranges averaged 1.6 (0.7-2.9) km^2, and overlapped extensively. Lateral exit movement from the upper plateau into Koukouai gulch was established. The diel activity pattern was biphasic, with high activity in early morning and late afternoon.

High juvenile mortality and a shorter ecological longevity characterize this population. The median age was 16.2 months; male:female:juvenile ratio was 2.6:2.8:1. Breeding occurs throughout the year. Prenatal survival was less than 73.3%, while postnatal survival from birth to six months was 40%. The factors which could limit abundance were categorized into those that act on: (1) juveniles, (2) adults in their second year, and (3) older animals. Accidental mortality, miring of the young, habitat factors and mongoose predation were identified as the sources of juvenile mortality. Metastrongyllid and kidney worm infection were considered important direct and indirect causes of adult mortality. Failure of dentition appears to be the most likely process limiting the lifespan of individuals.

Chemical blood analyses revealed neutrophilic leukocytosis in the population. The pathologic condition was a probable consequence to some disease factor, microbial milieu in the habitat or to nematode parasitism.

A 17-month mark-recapture program in the upper-plateau koa, ohia and lower plateau forests yielded a population estimate of 100-300 pigs, a catch success of 1.8 pigs per 100 trap nights. Density and trappability varied among forest types. Visitation frequency to trap sites averaged 17.5% of total trap nights.

Management is recommended principally because the feral pig disrupts and destroys native forests and replaces the native ecosystem with the exotic strawberry guava, which it effectively disperses. The management recommendations proposed herein incorporate a built-in eradication strategy to free the Valley of pigs and emphasize an integration of various control methods to maximally impact both young and old animals.

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CHAPTER 1

INTRODUCTION

The introduction of hoofed mammals into natural ecosystems not previously supporting them is one of man's activities which adversely affects the stability, organization, and productivity of biotic communities (de Vos et al. 1956; McKnight 1964; Fosberg 1977). Motivated by a desire for nostalgia, increased food resources, sport hunting, stock improvement, pest management and other reasons, exotic wildlife introductions have often been intentional, but are sometimes accidental. In the days of colonists and explorers, transport of domestic livestock as ship's stores and their subsequent introduction and release in new lands were standard practices. Frequently, animals were liberated on uninhabited shores "to multiply and become useful to navigators who might visit the coast" (Baudin in Cooper 1954).

One hoofed mammal widely transported, introduced world-wide, and left to multiply was the pig, Sus scrofa Linnaeus (1758). Whether it was introduced in its wild, domestic, or feral states, the pig often has adapted remarkably well, and in a relatively short period of time, to a new environment by establishing breeding populations. Examples of firmly established populations can be seen on both continents and islands.

In the continental United States, there were two phases of introduction, an early one involving the domestic pig and a later one of the European wild boar, a naturally wild species. The wild boar was first introduced in 1912 and is now established in at least four states (Stegmen 1938; Shaw 1940; de Vos et al. 1956; Jones 1959; Laycock 1966; Bump 1970; Godin 1977; Barrett & Pine 1980). Domesticated pigs were introduced in 1539 (Towne & Wentworth 1950). By 1945, feral pigs were reported from 17 southern states (McKnight 1964) and were the most numerous feral ungulate in North America. Presently, feral populations are found in all of the Southeastern states (Wood & Lynn 1977, Wood & Barrett 1979), in California (Barrett 1977, 1978; Barrett & Pine 1980), 19 National Wildlife Refuges (Thompson 1977) and in nine National Parks (Singer 1981).

Outside the continental land mass of North America feral pigs have become well established on Santa Rosa, Santa Cruz, and Santa Catalina islands, California (McKnight 1964); on Ossabaw and Cumberland islands, Georgia (Smith et al. 1980; Singer 1981); on Horn and Gulf, islands, Mississippi (Baron 1980); on Robert's Island, Canada (Smith & Hawkes 1978); in the West Indies (Wiewandt 1977); and in Latin America (Petrides 1975). In the Pacific region: Santa Cruz, Floreana and San Salvador of the Galapagos Islands (British Admiralty 1943; Kruska & Rohrs 1974); Australia (McKnight 1976; Tisdell 1979, 1980a,b; McIntosh & Pointon 1981); New Zealand (Wodzicki 1950); Marianas (Wheeler 1979); Swain, Tokelau islands (Kirkpatrick 1966); Hawaiian Islands (Tomich 1969; Kramer 1971); on several coral islands (British Admirality 1943); and many other Pacific islands (British Admirality 1943, 1944, 1945a,b). Feral populations in these areas have radically different histories, but typically they originate from domestic stock, which has turned feral.

An exception is that on Robert's Island, Canada, where a 10-year-old population was established from a stock of nine feral pigs imported to that site.

It is well known by ecologists and environmentalists that pigs feralize easily, undergo eruptions in numbers, and are disruptive components of native ecosystems. This ease of adaptation to the wild and, in particular, of rapid population increase may be attributed to innate characteristics. Among ungulates, the pig is perhaps the most adaptable species and is a prolific breeder capable of producing two large litters a year. It is both a food and habitat generalist (Bratton 1974). These aspects of the pig's ecology have allowed it to adapt readily to a feral existence in a wide range of habitats.

Following introduction, the population ecology of an exotic ungulate is relatively predictable (Elton 1958, 1966; Riney 1964). According to Riney (1964) and Caughley (1970, 1977), the population history of an exotic population passes through an initial establishment phase, followed by a single eruption and finally fluctuation to extinction or to some kind of resting or nonresting stability with the environment. Characteristic of all exotic introductions including the pig, is the lack of attention or import given to an introduction until numbers become high or individuals become dispersed. Concerns for control, containment or eradication only then become urgent. Consequently, little is known about the population processes and habitat responses during the period of initial increase in population size.

World-wide evidence shows that feral pigs in new environments generate complex ecological and socio-economic problems (Wodzicki 1950; Howard 1964; Challies 1975; McKnight 1976; Barrett 1979; Tisdell 1979; Wood & Barrett 1979; Barrett & Pine 1980; Hone & O'Grady 1980). The feral pig has been declared a noxious animal, vermin, or pest in many countries. It is extremely disruptive to native fauna and flora. It alters species composition and upsets the stability of natural ecosystems (Bratton 1974; Baker 1975, 1979). Under insular conditions, perturbations are more severe, and destructive but less understood than in continental areas. In many instances management has been difficult or impossible. Consequently management and control of pig populations have become imperative in many of the above-mentioned areas.

As pointed out by Fosberg (1963) and Carlquist (1965, 1974), island ecosystems are unique due to their isolation, reduced species competition, high endemism, and extreme vulnerability to disturbance. In addition, the disruption of an insular ecosystem, unlike those in continental areas, once begun is often unidirectional and irreversible even when given time to recover or when remedial management is applied (Leopold 1969; Fosberg 1977). The Hawaiian archipelago, is a prime example of an oceanic island chain where biotic community response and tolerance to feral ungulate activity can be investigated. The pig and other terrestrial quadrupeds were not present in the islands in prehuman times; the only native mammals were the hoary bat, Lasiurus cinereus, and the monk seal, Monachus schauinslandi, (Tomich 1969). Having evolved in the complete absence of mammalian herbivores, the vegetation lacks many antiherbivore defenses such as thorns or harsh foliage, is noticeably nonpoisonous, and is particularly fragile and susceptible to animal trampling, rooting and grazing. With this evolutionary history in mind, an investigation of feral ungulate ecology in an insular environment may be considered a special case study.

Much of the research interest in feral ungulates in both island and continental areas is aimed at obtaining information concerning impacts on habitats and the population dynamics, with the object of improving the management of wildland resources. This study of the feral pig in a pristine montane rain forest in Kipahulu Valley (hereafter referred to as the Valley), Haleakala National Park, Maui, also has a management objective. The Valley was described by a Nature Conservancy sponsored Scientific Expedition as a sanctuary for many rare species and a "unique natural laboratory available nowhere else on earth for the study of endemism, ecological genetics, pedogenesis, and the complexities of pristine ecological systems" (Warner 1967). They also found feral pigs which the Expedition identified as the primary destroyer of the rain forest ecosystem.

The Valley's pig population had its genesis in the 1940's (see Chapter 5) and is a relatively late arrival at this site. Ranging into the rugged, and remote, closed-canopy rain forest, the feral pig thrived. Several factors may have contributed to its continued feral existence. These are examined below to help formulate a testable hypothesis.

Since its inclusion, in 1969, as a wilderness area within Haleakala National Park, the Valley has been closed to hunters and the public. The pigs in the Valley have therefore been protected from hunting. There are no known predators; the only other mammals living in the region are a mongoose, *Herpestes auropunctatus*, three rats, *Rattus rattus*, *R. norvegicus*, and *R. exulans*, and the house mouse, *Mus musculus*; all small introduced species. The pig is therefore a terminal member in the food chain in this biotic community. In addition the rain forest environment is favorable for pigs in three ways. First, there is no interspecies competition between the pigs and other mammals (Giffin 1978). Second, the vegetation is green and luxuriant all year suggesting that food and cover may not be limiting factors. The continued feral existence suggests that the ecological requirements of the pigs, which permitted the original establishment in the wet forest, are met adequately. Third, water, a critical resource for pigs in some habitats, is never limited in the Valley, even during summer. With these theoretical considerations in mind, it is hypothesized: (1) that the quantity of food, cover and water are not important in limiting population processes, and (2) population regulation comes about through food quality rather than competition for food and is more likely to be exerted from below rather than from above, because of protein dilution in plants (White 1978).

For this study, a choice of approaches was available to me; the natural history approach as outlined by Elton (1966) was adopted. In the Valley, where biological resources, other than those reported by the

1967 Scientific Expedition, have not yet been inventoried and are poorly understood, the natural history approach was considered most desirable for this study. My objectives were to investigate the population biology and ecological interrelations between the pig and its habitat. The overall goals were few but specific. First, because of the specific information needs of the National Park Service particularly with regard to control programs, this study seeks management-related information as a basis for management recommendations. Second, the study is designed to explain observed habitat changes and to predict future patterns. Third, it is intended to examine any population process that might be unique to a topographically closed rain forest ecosystem. Finally, while significant information on feral pigs has been accrued from studies elsewhere, one apparent conclusion is that pigs are extremely adaptable and ecological relations in pig populations differ from one locale to another. Sufficiently detailed studies are lacking in closed tropical forest habitats like the Valley. Thus, the present study should contribute to an understanding of pigs in this different area.

CHAPTER 2

LITERATURE REVIEW

Semantics

(a) Pig, swine, hog, boar

The terms pig, swine, hog, and boar have been variously applied to all suids in their various states of existence, in a general, genitive sense or as distinguishing epithets. Pig and hog, but not swine have been applied to wholly unrelated nonsuid species (Skeat 1924; Mellen 1952). The origin of these terms is unknown. Hog has been accorded a Celtic origin and is thought to originate from either a Hebrew word meaning "to surround" or from the Arabic verb "viz," meaning "to have narrow eyes" (Miller 1976). In its original usage, pig refers merely to size, more specifically to the young or suckling of a suid which has not reached sexual maturity (Weekley 1952; Skeat 1924; Onions 1952). Extending this definition, it follows that sow and boar be applied to suids reaching sexual maturity and that suids before the breeding age be referred to as either a male or female pig. Hog was originally applied referring to age, that is, suids of the second year (Onions 1952) or weighing more than 55kg and reared for the purpose of slaughter (Standard Encyclopedia Dictionary 1968; Guralnik 1970).

The distinction between hog and pig appears to be one of domesticity and age or size. Swine refers to a domesticated suid (Standard Encyclopedia Dictionary 1968; Onions 1952). Its original usage may have been either generic or restricted to a domesticated suid. Since only one suid species, S. scrofa, has been domesticated, it follows, by definition, that the application of the term swine to the other seven suid species becomes invalid. According to Onions (1952), swine has been superseded in common use by pig or hog. The term boar when used as wild boar, European wild boar, or the boar generally carries a specific meaning and refers to the Palearctic-Asiatic species, S. scrofa, or any of its subspecies. Otherwise it is applied to mean a sexually mature male suid.

Clear examples of the original usage of pig and hog before the 19th century, though rare, can be gleaned from the journals of several explorers. In his journal entry on September 18, 1777, Cook wrote that he received "a hog, a pig and a dog" as a present from servants of a chief on the Society Islands (Cook 1784, Vol. II, p. 57). When receiving pigs from natives, Cook frequently records them as "small pig" or "large hogs."

In trading with the natives, "a small pig of 10 or 12 pounds" was traded for a spike, but "a hog" was exchanged for a hatchet (Cook 1784, Vol. I, p. 82). Although hog and pig have been used in an archaic sense for other animals (Skeat 1924; Mellen 1952), it is improbable that Cook had used pig or hog for another animal. The only quadrupeds present at the time of his visit were dogs, pigs and rats (Cook 1784, Vol. III, p. 118) and the fowl had never been termed as a hog. Ellis' (1831) usage of the terms hog, swine, pig in his journals was close to the original meanings. Present day usage of pig, hog, swine does not follow any established rule. The literature shows that the same author, working on the same population of pigs in the same location, has on different occasions used hog, swine or pig. Subject disciplines, biogeographical regions and not to mention personal preference often influence the use of these terms. In the field of vertebrate zoology pig is applied to suids in their wild, domestic and feral states, whereas hog or swine is more commonly used in agricultural and veterinary sciences (Lapedes 1978). Looking at geographical regions alone, pig is applied almost exclusively to feral, wild and domestic suid populations in the Australasian, Indo-Malaysian, Asian, African and Pacific areas. In the continental United States, all three terms, hog, swine and pig, in this order of frequency, are used to describe domestic, feral and wild populations.

It is apparent therefore that pig is more widely used than hog or swine. Although all these terms appear to be acceptable, pig is undoubtedly more genitive in the zoological sense (my bias), and its usage is probably more desirable than the other terms. Perhaps the genitive suid should be used when there is doubt. In this thesis, pig is used in the descriptive and genitive sense depending on context.

(b) Wild, feral, domestic, pariah

Four possible states of existence--wild, domestic, feral and pariah--may be described for pigs in various environments using the following two criteria: (1) the extent of influence by man on the gene pool and, (2) the action of natural selective forces. No taxonomic distinctions exist among pigs in any of the four states defined below, all of which have been given the same specific designation, Sus scrofa.

A wild population is one which has no history of exposure to a domesticator population, and therefore has not been under the influence of artificial selection by man. The present and future gene pool of a wild population are under the direct control of natural selection (Brisbin et al. 1977; Brisbin 1977). When the natural forces acting on a wild population are removed or modified by man, a domestic population results. Thus a domestic pig population is one whose ancestral gene pool has been modified by the process of artificial selection. Modern man continues to modify the ancestral gene pool by intense artificial selection. This has resulted in the production of 87 recognized breeds of domestic pigs and another 225 breed-types (Pond & Houpt 1978). When man's existing influence on the future gene pool of a pig population is slight or negligible, as when a loose association develops between the pig and man near settlement areas, then a pariah population may be described (Epstein 1971; Brisbin 1977). In a pariah population, the future genetic composition of the population is determined by breeding patterns which are influenced, but not completely controlled, by man. True pariah pig populations probably exist near aboriginal settlement areas in the forests of the Indo-Malaysian region, and in the Pacific islands. Although Rappaport (1967) did not use the term pariah in his writings, the existence of true pariah pig populations among the primitive New Guinea highlands can be inferred from his studies. Feral pigs are those which originate from domestic stock but have reverted from domesticity to become free-living and no longer depend on man for sustenance or breeding (Pullar 1953; Kruska & Rohrs 1974; McKnight 1976). Consequently, the gene pool of a feral pig population differs from that of its wild ancestor in that its ancestral gene pool had at some point in the past been modified by artificial selection imposed on it by man. By its return to a wild state existence the feral population is reexposed to natural selection which now acts on its future gene pool.

It is evident, therefore, that each of the four states of existence has a precise definition of evolutionary significance. Unfortunately, usage of wild and feral are less than precise, and have been used interchangeably or synonymously to mean "living in the natural environment." Wild is commonly used in the vernacular sense to encompass both wild and feral states of existence (Wood & Barrett 1979; Barrett & Pine 1980). This disregard for usage of precise terms is probably inconsequential to the utilitarian hunter or sportsman, but may present ambiguity and problems to the law-enforcement officer, forensic veterinarian, connoisseur, or a biologist working in an area where pigs exist in more than one of the described states. The Asiatic wild pig, *S. scrofa*, in Peninsular Malaysia (Diong 1973) has, for example, been cited as "feral hog" by Wood and Brenneman (1978) and as "feral pig" and "wild pig" by Pavlov (1980). In this dissertation the various states of existence are used as defined above in their evolutionary sense and "free-ranging" when used, is applied to encompass both feral and wild populations.

In conclusion, the proliferation of somewhat questionable descriptive epithets for the feral pig in Hawaii such as the following might be pointed out here: "Hawaiian pig" (Warner 1959; Nichols 1962; Whitten 1977; Titcomb 1978); "Hawaiian pigs" (Hawaiian Audubon Society 1981); "Hawaiian wild pig" (Giffin 1977); "Hawaiian wild boar" (Swedberg 1963); "feral Hawaiian pig" (Wilson & McKelvie 1980); "wild pig in Hawaii" (Barrett-Connor et al. 1976); "wild pigs" (Bryan 1937; Tillett 1937; Tinker 1938; Vitousek 1941); "native pig" (Luomala 1962). The descriptive phrase "feral pig in Hawaii" or "Hawaii's feral pig" are preferred over those above. Use of the descriptive "Hawaiian" whereas valid when applied to the endemic seal, bat or fruitflies, is unsuitable when applied to the pig, as the qualifier "Hawaiian" connotes indigenousness. The pig first brought in by the Polynesians should be referred to as "the pig of the indigenous people," "the native's pig" or more aptly the "Polynesian pig."

The Pig

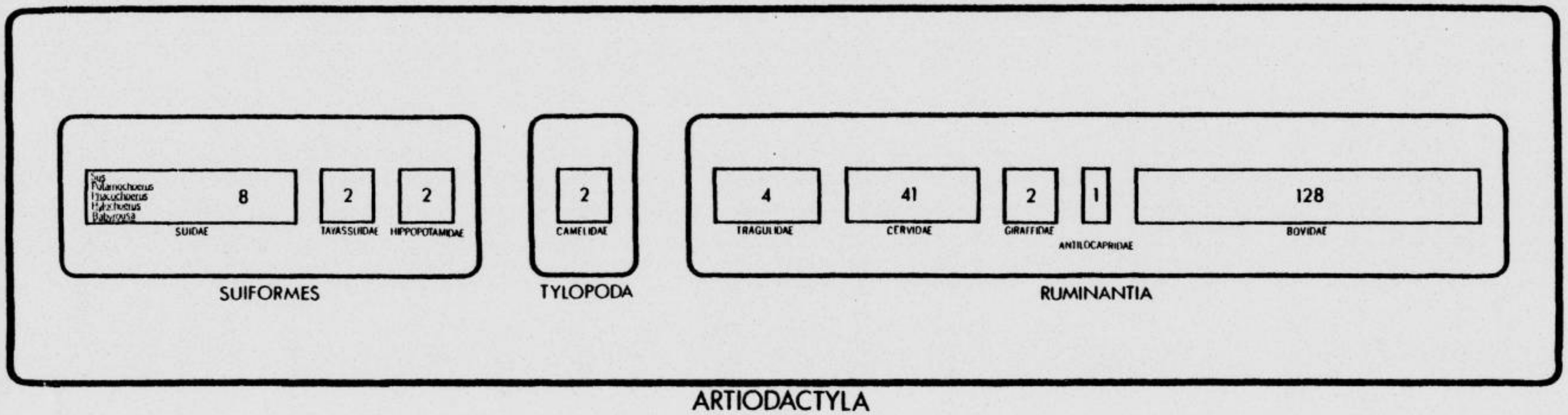
(a) Classification, nomenclature, and distribution

The evolution and phylogenetic relationships of pigs have been reviewed by Mellen (1952), Simpson (1945) and more recently by White and Harris (1977) and Kingdon (1979) for African species. Ancestors of pigs arose from Condylarths by the early Eocene via the primitive palaeodonts. Wholly native to the Old World, pigs as a group have sometimes been termed "old pigs" with the antithesis "New World pigs" applied to peccaries. Although Simpson (1945) considers peccaries as an offshoot of the Old World stock, peccaries are anatomically (Fradrich 1972) and immunologically (Duwe 1969) more related to present day ruminants than to pigs, which they only superficially resemble in appearance and behavior. The application of pig to peccaries is therefore invalid; the application of Old World to pigs is redundant, and ambiguous as it, like "true pigs," insinuates existence of the corresponding antithesis "New World" for another group of pigs.

The classification of modern day Artiodactyla, to which pigs and all other hoofed mammals belong, can be illustrated with a venn diagram (Figure 1). There are a total of 190 species, 92 of which are indigenous to Africa (Morris 1965). The affinities and differences among the nine families which are distributed in three orders have been reviewed by Haltenorth (1963). Within the suborder Suiformes, the family Suidae is represented by eight extant species. The East Asiatic pig, S. s. vittatus, was for a long time thought to be a distinct species, but vittatus has been reduced to a subspecies (Haltenorth 1963; Ellerman & Morrison-Scott 1966; Fradrich 1972). Therefore using venn notations, Suidae (pigs) = {Sus scrofa (common wild pig), Sus barbatus (bearded pig), Sus verrucosus (Javan pig), Sus salvanius (pigmy pig), Babyrousa babyrousa (babirusa), Phacochoerus aethiopicus (wart pig), Hylochoerus meinertzhageni (giant forest pig), Potamochoerus porius (bush pig)}.

Nomenclature of pigs has been problematic and difficult (Allen 1940; Heptner et al. 1966; Hoogerwerf 1970). This is because taxonomic studies have been complicated by the fact that pigs, in particular S.

Figure 1: Venn diagram classification of modern day Artiodactyla. ▬▬▬ - Order; ━━━ - Suborder; ─── - Family. Numerals within family subsets indicate number of species.


Sus
Potamochoerus
Phacochoerus
Hylochoerus
Babyrousa
8
SUIDAE
2
TAYASSUIDAE
2
HIPPOPOTAMIDAE
SUIFORMES
2
CAMELIDAE
TYLOPODA
4
TRAGULIDAE
41
CERVIDAE
2
GIRAFFIDAE
1
ANTILOCAPRIDAE
128
BOVIDAE
RUMINANTIA
ARTIODACTYLA

scrofa, are an extremely morphologically variable and adaptable group throughout their range. Geographic races differ in morphology, behavior and anatomy. Quite naturally, therefore, overzealous naturalists have described "species" within one group of pigs (Allen 1940) or from studies on a very limited number of skull samples (Medway 1965). The lack of consensus on characters which should be regarded as taxonomically distinct of the species and those characters that could have arisen as a result of isolation and adaptation have lead to an inevitable proliferation of "species" names. Fortunately, the generally accepted working definitions of species, race, and breed have helped in taxonomic studies of pigs.

Heretofore, museum studies have contributed significantly to pig taxonomy, but recent immunogenetic studies have demonstrated the potential of such methods in pig taxonomy and in elucidating evolutionary and pylogenetic relationships among suid species (Kurosawa et al. 1979). Most taxonomic work, however, has been done on S. scrofa, the only Palearctic species, although there has been recent interest in African species (D'Huart 1978 in Barrett 1980; Kingdon 1979). Nothing is known about the geographic races or subspecific composition of present day feral pigs in the Pacific region. In Europe, biologists working on pigs, generally adopt the systematics as used by Haltenorth (1963), but considerable discussion has since arisen and a complete taxonomic review of Suidae is more than necessary (Fradrich 1981 Berlin, Germany - pers. comm.). Bratton (1977) attempted a review on the nomenclature of the Palearctic species, but her work is very incomplete, most of which is cited generously from Heptner et al. (1966).

The recognized species and subspecies of pigs from the works of European, American and Asian taxonomists are listed in Table 1. Subspecific listing by Haltenorth (1963), and those not listed by other authors have in every case been checked, consulted and cross-referenced with at least two other (where available) regional authorities, for verification on the validity of subspecies recognition. Despite this approach, it should be pointed out that the subspecific listing (Table 1) should not be considered as final or complete, pending further work on suid taxonomy using conventional skull samples or more recent biochemical and serological methods mentioned above. Notwithstanding this, it can be seen that Suidae is represented by 81 subspecies. *Sus* is represented by four species, *S. scrofa* with 35 subspecies, *S. verrucosus* with 13 subspecies, *S. barbatus* with six subspecies, and *S. salvanius*, where nothing is yet known about its subspecific composition in its present range. *S. s. scrofa*, the continental wild pig and typical form of Linnaeus species (Bradford 1912), is also referred to as German wild boar; its other synonyms are *setosus*, *ferus*, *europeus*, *aper*, and *celtica* (Bradford 1912; Haltenorth 1963; Ellerman & Morrison-Scott 1966; Heptner et al. 1966). *Babyrousa*, *Phacochoerus*, *Hylochoerus* and *Potamochoerus* are each represented by one species, with four, seven, three, and 13 subspecies respectively. *Hylochoerus meinertzhageni* is the largest species, whilst *S. salvanius*, the smallest, was rediscovered in 1971 and is the only pig to be accorded Endangered status (Oliver

TABLE 1: Nomenclature, synonyms, common names and distribution of wild pigs.

Taxon	Synonyms /Common Names	Distribution	References	Remarks[a]
Sus				
S. *scrofa* Linnaeus (1758)				
S.*s*. *andamanensis* Blyth '1858)	Andaman wild pig	Andaman islands, S.E. Asian islands	1,2,4	a feral pig
S.*s*. *ussuricus*	Northeastern Chinese wild boar	Amur, Northeastern China	4	valid subspecies
S.*s*. *attila* Thomas (1912)	Transcaucasian wild pig	Caucasus	1,2,4,6,7	valid subspecies
S.*s*. *barbarus* Sclater (1860)	*algira*, *sahariensis*, *algirus*, North African wild pig	Algeria, Morocco, Tunisia	2,4	valid subspecies, correct name is *algira*
S.*s*. *castilianus* Thomas (1912)	*baeticus*, Spanish wild pig	Iberian Peninsula, Spain	1,2,4,7,8	synonym of *scrofa*, *baeticus*
S.*s*. *chirodontus* Heude (1888)	*melas*, *chirodonta*, *palustris*, *chirodonticus*, *leucorhinus*, *flavescens*, South China pig	Southern China, S.E. Asian islands	1,2,3,4,5	synonym of *moupinensis*
S.*s*. *coreanus* Heude (1897)	*koreanus*, Korean wild boar	Korea	1,2,4	synonym of *ussurious*
S.*s*. *cristatus* Wagner (1839)	*typicus*, *aper*, *indicus*, *bengalensis*, Indian wild boar	S.E. Asia	a,2,4,6,24	valid subspecies
S.*s*. *domesticus* Linnaeus (1758)	domestic pig, feral, pariah pig	Cosmopolitan	23	valid subspecies
S.*s*. *falzfeini* Matschie (1918)	Polish wild pig	Poland	1,2,4,7	synonym of *attila*
S.*s*. *floresianus* Jentink (1905)	Flores wild pig	Flores, S.E. Asian islands	2,4	a feral pig
S.*s*. *jubatulus* Miller (1906)		Peninsula Malaysia, Langkawi	12	synonym of *vittatus*
S.*s*. *jubatus* Miller (1906)		Thailand, Indochina, Peninsula Malaysia, Burma	1,2,10,12,24	synonym of *vittatus*
S.*s*. *leucomystax* Temminck (1842)	*japonica*, Japanese wild boar	Japan	1,2,4,6,9,23	valid subspecies
S.*s*. *libycus* Gray (1868)	Asia Minor pig	Southwestern Asia Minor	1,2,4,6	valid subspecies
S.*s*. *majori* De Beux & Festa (1912)	Italian wild pig	Italy	2,4,7	synonym of *scrofa*
S.*s*. *meridionalis* Forsyth-Major (1882)	*sardous*, Sardinian wild boar	Sardinia	1,2,4,7	valid subspecies
S.*s*. *milleri* Jentink (1905)	Java wild boar	Java, Bali	2	synonym of *vittatus*
S.*s*. *moupinensis* Milne-Edwards (1871)	*oxyodontus*, *dicrurus*, *curtidens*, *paludosus*, *planiceps*, *collinus*, North China pig	Northern & Middle	1,3,4,5,6	valid subspecies

TABLE 1 (continued)

Taxon	Synonyms/Common Names	Distribution	References	Remarks[a]
S.s. natunensis Miller (1901)		Natuna	2	status unsure
S.s. niadensis Miller (1906)		Indonesian islands	2	status unsure
S.s. nicobaricus Miller (1902)		Nicobar islands	1,4	a feral pig
S.s. nigripes Blanford (1875)	central Asiatic wild boar	Russia, Middle Asia Mongolia	1,2,4,6	valid subspecies
S.s. papuensis Lesson & Garnot (1826)	Papuan pig	New Guinea, Melanesia & other Pacific islands	2,4	hybrid of S.s. vittatus and S.celebensis
S.s. peninsularis Miller (1906)	Malayan wild pig	Peninsular Malaysia	5,12	synonym of vittatus
S.s. raddeanus Adlerberg (1930)	sibircus Staffe (1922), planiceps, raddeana	Mongolia, China	1,3,4	valid subspecies
S.s. reiseri Bolkay (1925)	reizeri, Yugoslavian wild pig	Yugoslavia	1,2,4,7	synonym of libycus
S.s. rhionis Miller (1906)	andersoni	Riau archipelago	2	synonym of vittatus
S.s. riukiuanus Kuroda (1924)	Riukiu islands wild boar	Riukiu islands	1,2,9	valid subspecies
S.s. sennaarensis Gray (1868)	Egyptian wild boar	Northern Africa	2,6,13	a feral pig
S.s. scrofa Linnaeus (1758)	setosus, ferus, europaeus, aper, celtica, scropha, central European wild boar	Western Europe, North Africa, Russia	1,2,4,6,7, 8,23	valid subspecies
S.s. taivanus Swinhoe (1863)	Porcula taivana	Taiwan	1,2	valid subspecies
S.s. timorensis Muller & Schlegal (1845)	Timor wild pig	Timor, S.E.Asian islands	2,4	synonym of S.celebensis
S.s. ussuricus Heude (1888)	continentalis, canescens, gigas manchurias, songaricus, Far Eastern pig	Siberia, China	1,2	valid subspecies
S.s. vittatus Boie (1828)	vittatus Muller & Schlegal (1842), East Asiatic wild boar, Sunda wild pig	Peninsula Malaysia, S. E. Asia	2,4,6,11	valid subspecies
S.s. davidi nov		N. W. India, Pakistan, Iran		valid subspecies
S. salvanius Hodgson (1847)	Porcula salvanius, P. salvania	Nepal, Sikkim, Bhutan, Assam	2,14	valid species
S. verrucosus Muller & Schlegal (1842)				
S.v. amboinensis Major (1897)		Amboina islands	15	synonym of S.celebensis
S.v. borneesis Major (1897)	barbatus	Borneo (as feral populations)	15,16	synonym of verrucosus

TABLE 1 (continued)

Taxon	Synonyms/Common Names	Distribution	References	Remarks[a]
S.v. cebifrons Heude (1888)		Cebu, Philippines	2,15	valid subspecies of S. barbatus not of verrucosus
S.v. celebensis Muller & Schlegal (1845)		Celebes	2,11,15,23	a distinct species; no subspecies
S.v. ceramicus Gray (1868)		Ceram island	2,15	synonym of verrucosus
S.v. inconstans Heude (1892)	mindanensis	Mindanao island	2	synonym of S.barbatus philippensis
S.v. maritimus Heude (1899)		South Celebes	2	synonym of S.celebensis
S.v. minutus Heude (1888)		Luzon	2,15	synonym of S.barbatus philippensis
S.v. negrinus Sanborn (1952)		Luzon	2	synonym of S.barbatus cebifrons
S.v. olivieri Sody (1941)		Madurs	2	synonym of verrucosus
S.v. philippensis Nehring (1896)		Philippine islands	2,15,16	valid subspecies of S.barbatus, not of S.verrucosus
S.v. verrucosus Muller & Schlegal (1842)	Javan pig	Java	2,15,16	valid subspecies
S.v. weberi Jentink (1905)		Saletar islands	2	synonym of S.celebensis
S.v. blouchi nov		Bawean islands		valid subspecies
S. barbatus Muller (1838)				
S.b. ahoenobarbus Huet (1888)		Palawan, Busuanga	2	valid subspecies
S.b. balacensis Major (1897)		Balabak	2	synonym of ahoenobabus
S.b. barbatus Muller (1838)	longirostris, gargantus, Bornean bearded pig	Borneo	2,11,17,18, 19,23,24	valid subspecies
S.b. calamianensis Heude (1888)		Calaman		synonym of ahoenbarbus
S.b. oi Miller (1902)		Peninsula Malaysia, Sumatra, Riau archipelago		valid subspecies
S.b. sumatranus Rehn (1939)	Sumatran bearded pig	Sumatra	2	synonym of oi
Babyrousa				
B. babyrusa Linnaeus (1758)	Babirusa			
B.b. babyrousa Linnaeus (1758)		Moluccas, Buru, Sula islands	2,6	valid subspecies
B.b. cerebensis Deninger (1910)	alfurus	Celebes	2,6	valid species
B.b. frosti Thomas (1920)		Sula islands	2	synonym of babyrousa
B.b. tongeanensis Sody (1949)		Malengi	2	valid subspecies
B.b. bolabotuensis Hooijer (1952)		central and south Celebes		valid subspecies

TABLE 1 (continued)

Taxon	Synonyms/Common Names	Distribution	References	Remarks[a]
Hylochoerus				
H. meinertzhangeni Thomas (1904)				
H.m. ivoriensis Bouet & Neuville (1930)		Ghana	2,10	
H.m. meinertzhageni Thomas (1940)	ituriensis, gigliolii, schulzi	Uganda, Kenya	2,6,20,21	
H.m. rimator Thomas (1906)		Cameroon	2	
Phacochoerus				
P. aethiopicus Pallas (1767)				
P.a. aeliani Cretzschmer (1826)	centralis, massaicus, de lamerei	Nairobi, Abyssinia	2,21	
P.a. aethiopicus Pallas (1767)		Natal, central and east Africa	2,6,11,23	in need of revision;at least a West and East African form can be distinguished.
P.a. africanus Gmelin (1767)		West Sudan, Guinea	2,6,11,22,23	
P.a. buto Heller (1914)	barkeri	Sudan, Uganda	2	
P.a. fossor Schearz (1913)		West Africa	2,6	
P.a. shortridgei St. Leger (1932)			2	
P.a. sundevalli Lonnberg (1908)		Natal,central and east Africa	2	
Potamochoerus				
P. porcus Linnaeus (1758)				
P.p. albifrons Du Chaillu (1860)		Equatorial Africa	2	
P.p. albinuchalis Lonnberg (1920)		Equatorial Africa	2	in need of revision; may be divisible into two species: P.porcus(albifrons, albinuchalis, congicus, pictus), of the forest belt of west and central Africa; and P.larvatus(daemonis, hassama, hova, koiropotamus, nysae, somaliensis, ubangensis), of the bush country of East and South Africa and Madagascar. The first
P.p. congicus Lonnberg (1910)		Congo	2,6	
P.p. daemonis Major (1897)	intermedius, keniae, arrhenii	Nairobi	2,21	
P.p. hassama Heuglin (1863)		Ethopia	2,6	
P.p. hova Lonnberg (1910)		Madagascar	2	
P.p. koiropotamus Desmoulins (1831)		South & East Africa	2,6,11,13,23	
P.p. larvatus Cuvier (1822)		Madagascar	2,6,13,20	
P.p. nysae Major (1897)	johnstoni, maschona, cottoni	Malawi	2,6,13	
P.p. pictus Gray (1852)		Cameroon	2,6,11,23	

TABLE 1 (continued)

Taxon	Synonyms/Common Names	Distribution	Reference	Remarks[a]
P.p. porcus Linnaeus (1758)	*penicillatus*, *guineensis*	Ghana	2,6,20,22	is called the Red river hog, the second, the bush pig.
P.p. somaliensis De Beaux (1924)		Somalia	2	
P.p. ubangensis Lonnberg (1910)	*mawambicus*	Zaire	2,6	

Key to References:

1. Ellerman & Morrison-Scott (1966)
2. Haltenorth (1963)
3. Allen (1940)
4. Heptner et. al. (1966)
5. Tate (1947)
6. Leister (1939)
7. Haber (1969)
8. Bradford (1912)
9. Kurosawa et.al. (1979)
10. Robinson & Moulton (1922)
11. Miller (1897)
12 Medway (1969)
13. Dorst (1970)
14. Oliver (1980)
15. Major (1897)
16. Schwarz (1940)
17. Chasen (1940)
18. Medway (1965)
19. Banks (1931)
20. Kingdon (1979)
21. Maberly (1966)
22. Prunier (1946)
23. Grzimek (1972)
24. Miller (1906)

[a] Notes provided by Dr. Colin Groves, Australian National University, Canberra, Australia- per. comm. 1982

1980). *Porcula*, the generic name proposed by Hodgson in 1847 because of its small size, reduced tail and three pairs of mammae, is an accepted subgenus (Ellerman & Morrison-Scott 1966), but opinions on this differ (Oliver 1980). Except for *S. verrucosus*, *S. barbatus*, and *B. babyrousa*, all the other pigs have been studied in the wild by at least one modern ecologist (Barrett 1981).

Taxonomically, species characteristics in Suidae are well defined, but ecologically the group shares many features in common (Table 2). *Sus* adult dentition, $I\ \frac{3}{3}\ C\ \frac{1}{1}\ P\ \frac{4}{4}\ M\ \frac{3}{3} = 44$, distinguishes this genus from other genera of pigs, all of which have reduced dentition. The number of nipples has hitherto been used as a taxonomic character, but Rana's (1977) observation that nipple numbers in the Indian wild boar are proportionate to the animal's size has led Sakya (1979) to discredit the use of nipple numbers to taxonomically separate pigmy pigs from wild pigs. *Sus* has six to seven pairs of mammae, are more prolific, have larger litters than other genera where there is a reduction in the pairs of mammae to two pairs in *Phacochoerus* and to a single pair in *Babyrousa*. *B. babyrousa* is considered a primitive species and not closely related to the other genera of pigs. Throughout its range, *S. scrofa* breeds freely with feral domestic pigs and its other races. Crossbreeds are interfertile. In Java and other Indonesian islands, *S. scrofa*, *S. verrucosus*, and *S. barbatus* overlap in their native range, but none of these species are known to interbreed. At the Gelsenkirchen Ruhr Zoo in West Germany, hybrids have been obtained from *S. barbatus* and the European wild pig, *S. scrofa*, but these hybrids do not breed.

TABLE 2: Comparison of some major characters among extant species of wild pigs.

	Sus scrofa	Sus verrucosus	Sus barbatus	Sus salvanius	Babyroussa babyrussa	Phacochoerus aethiopicus	Hylochoerus meinertzhageni	Potamochoerus porcus
Species characteristics	ears short, erect, without warts; well developed mane; boars with shields on shoulders	3 warts on each side of head	2 bushy tufts of hair on snout; pair of movable facial warts	ear hairless; reduced tail; without mane; endangered species; smallest pig	skin naked, smooth, wrinkled, almost hairless; grooving on snout; large canines	3 pairs of large warts on snout; distinct mane; drops on padded knees when feeding	prominent preorbital glands and cheek plates; well developed mane; largest living pig	long pointed ears, with tassels of hair pointed at tips; facial and carpel glands present
Nipples (pairs)	6	4	5	3	1	2	5	3
Pelage	bristled; dark grey, black, yellowish or brown; has undercoat of hair	black, grey	pale yellow, white	blackish to brown	black to greyish	dark brown to blackish	long black hair	russet brown to black with white markings on face, with yellowish hairs
Juvenile coat striping	longitudinally striped	indistinct when present	longitudinally striped	no striping	no striping	no striping	longitudinally striped	longitudinally striped
Adult dentition	$I^{3}_{3}\ C^{1}_{1}\ P^{4}_{4}\ M^{3}_{3} = 44$	$I^{3}_{3}\ C^{1}_{1}\ P^{4}_{4}\ M^{3}_{3} = 44$	$I^{3}_{3}\ C^{1}_{1}\ P^{4}_{4}\ M^{3}_{3} = 44$	$I^{3}_{3}\ C^{1}_{1}\ P^{4-3}_{4-3}\ M^{3}_{3} = 40\text{–}44$	$I^{2}_{2-3}\ C^{1}_{1}\ P^{2}_{2}\ M^{3}_{3} = 32\text{–}34$	$I^{1}_{3}\ C^{1}_{1}\ P^{3}_{2}\ M^{3}_{3} = 34$	$I^{1}_{2-3}\ C^{1}_{1}\ P^{3}_{2}\ M^{3}_{3} = 32\text{–}34$	$I^{3}_{3}\ C^{1}_{1}\ P^{4-3}_{4-3}\ M^{3}_{3} = 40\text{–}44$
Gestation length (days)	112-120	unknown	120	unknown, but less than for wild pig	120-150	170-175	125-150	120
Preparturition nest building behavior	present	present	present	present	present	present, uses subterranean holes and burrows	present	present
Litter size	4-6	4-8	2-8	3(2-6)	2, twins usually of same sex	2-8	2-6	3-6
Food habits	omnivorous, but eats animal food too	omnivorous	omnivorous	omnivorous	omnivorous	herbivorous; a grazer and less of a rooter; eats animal food too	herbivorous; grazer and less of a rooter	herbivorous, but eats animal food too
Habitats	forest, swamps, grasslands, agricultural areas, riverine habitats	dense forest, swamps, grasslands	tropical rain forest, swamps, riverine habitats	tall grass savannal, mixed dense scrub forest	forest, riverine habitats	savannah; light forest	dense forest; exposed habitats	dense forest; savannahs
Activity	nocturnal, crepuscular	nocturnal, crepuscular	nocturnal, diurnal	diurnal	nocturnal	diurnal	diurnal	nocturnal, crepuscular
Social organization	adult males solitary; family units; gregarious; migratory	family groupings; herds	migratory; gregarious, forming large herds; undergo periodic eruption	family groupings; adult males solitary	adult males solitary; small family groupings	adult males solitary; family groupings; small sounders	family and extended family groupings; adult males solitary; commercial latrines	family groupings; gregarious; large sounders; latrine system
References	Haltenorth (1963) Fradrich (1972)	Volz (1906) Leister (1939) Hoogerwerf (1970) Fradrich (1972)	Banks (1931) Medway (1969) Fradrich (1972)	Oliver (1980)	Haltenorth (1963) Fradrich (1972)	Dorst (1970) Fradrich (1972) Kingdon (1979)	Haltenorth (1963) D'Huart (1978) [Barrett 1980] Kingdon (1979)	Sowls & Phelps (1968) Dorst (1970) Kingdon (1979)

Preparturition nest building behavior is shared by all pig species. Longitudinal striping of the juvenile pelage, which appears to be a dominant species characteristic seen only in *S. scrofa* and its subspecies, has also been reported for *S. barbatus*, *Hylochoerus*, and *Potamochoerus*. There are, however, some discrepancies in the literature on the presence or absence of juvenile coat color, in species other than *S. scrofa*. All pigs are omnivorous, although vegetable matter makes up a greater bulk of the diet. Because of their rooting activity, predation on livestock and agricultural produce, pigs, particularly *S. scrofa*, *S. barbatus* and *S. verrucosus* have been variously classed as vermin, pests and noxious animals. Only *Babyrousa*, *Phacochoerus* and *Hylochoerus* are considered more grazers than rooters. All species have been hunted by natives and modern man for their meat, for sport and in the case of *S. salvanius*, for its skin.

The distribution of Suidae has been graphically illustrated by Murray (1866), Heptner et al. (1966), Haber (1969), and Mauget (1981) who have provided distribution maps for the wild boar. Ellerman and Morrison-Scott (1966) provide a complete area-listing on the former and present range of *S. scrofa* (Table 1). The Palearctic species has the most extensive range, extending from Western Europe to as far east as Japan, southward to North Africa, India, Sri Lanka and South-east Asia. Kingdon (1979), in a recent publication on East African Mammals, deals extensively with regional distribution of African pigs. Of the four Oriental species, *S. scrofa* has the widest distribution followed by *S. barbatus* which occurs principally in Borneo, Peninsular Malaysia, and

Sumatra. S. verrucosus has a smaller range, but overlaps with S. scrofa in most parts of its range. Babyrousa occurs principally in the Celebes and Sula Islands and because of its limited range, and human predation, is threatened with extinction. Considering all the pigs, S. salvanius probably has the smallest range, occurring in Nepal, Sikkim, Assam and Bhutan where most of its natural habitats have been destroyed by burning for agricultural purposes. The occurrence of free-ranging pigs outside their native range illustrates the success of prehistoric and modern man in rearranging the distribution of this ungulate species.

(b) Historical ecology of pig domestication

A species' susceptibility to domestication is largely determined by its social behavior, mating system, parent-young interactions, responses to man and food habits (Clutton-Brock 1976). Pigs are gregarious, form matriarchial social units (Barrett 1971), are omnivorous, can be reared easily, are docile and can, from Rappaport's (1967) observations, be imprinted on to humans when hand-reared from a young age. They are therefore good subjects for domestication. Only one species, S. scrofa, has been domesticated, however, the other species, especially the African species, are good potential domesticants (Kingdon 1979).

Recent palaeozoological studies have shown the first records of the domestication of the pig to be at Anatolia and Kurdistan, in prehistoric South West Asia by about 7000 B.C. (Reed 1959, 1969; Bokonyi 1969). The reduction in the length of the tooth row, especially the third molar in domestic pigs has been used as a reliable taxonomic indicator replacing the use of the lachrymal bone length (Zeuner 1963), to differentiate between domestic and wild pig populations. Using this taxonomic key, other studies have shown Europe, the Near East, China and South-east Asia as the other more recent centers for pig domestication. From their zooarchaeological studies, Olsen and Olsen (1980) believe China to be an early center for pig domestication; domestication probably having taken place here by 5000 B.C. (Mellen 1952). In South-east Asia and New Guinea, the pig was domesticated later in the Neolithic era, by about 3000 B.C. (Bellwood 1979). Pig domestication at these prehistoric domestication centers is associated with the establishment of settlements and the shift from the purely hunter-gatherer way of life to primitive agriculture and pastoralism. Open grazing and agricultural lands were important for the domestication process (Olsen & Olsen 1980). However, the keeping of young and adult animals as opposed to pastoralism is considered the most plausible prehistoric mode of pig domestication (Reed 1959). This practice can still be found today in aboriginal societies. Among tribal societies in the highlands of New Guinea, Rappaport (1967) observed how pigs were domesticated by human care and agriculture. In South-east Asia, pig domestication probably began with the capture, rearing and husbandry of different subspecies of S. scrofa, a practice which can still be seen among contemporary Orang Asli (Rambo 1979).

All available osteological and zooarchaeological studies suggest that pig domestication occurred at least several times and in many different areas from different wild populations and, hence subspecies, of the Palearctic-Asiatic ancestral species, *S. scrofa*. Parallel domestication for much of the Old World is very likely for the pig because of its wide distribution from Western Europe to the Atlantic fringe. The theory by Soule in Reed (1961) that the pig was first domesticated in Asia from *S. vittatus* (sic) and the domesticated stock transported westwards is no longer valid in the light of present studies and has been discounted by Reed (1959), but the importance of each domestication center acting as a diffusion center should not be discounted. Whether viewed in the prehistoric or the present context, domestication is not a discreet event, but a continuing process. Bokonyi (1969) identifies this process as being made up of three components--domesticator (man), wild ancestor (*Sus scrofa*), and the domesticant (domestic pig). Zeuner (1963) identifies the domestication process as being made up of the following stages: initial association, with free breeding, confinement, with breeding in captivity; selective breeding; breed improvement and extermination of the wild ancestor. The last of these stages is not yet true for the *S. scrofa* other than in Great Britain and Egypt.

Many different breeds are found world-wide today for various economic reasons. As Bratton (1977) correctly observed, all domestic breeds have been variously called *S. domesticus* and *S. s. domesticus*; the former specific designation is commonly used in the animal science literature (Pond & Houpt 1978). Specific designation of *S. domesticus* to domestic pigs would imply that the domestication of the pig from its wild progenator, *S. scrofa*, has created a new species. According to

Storer et al. (1979), domestication has never produced any new species. Therefore, designation of domestic pigs as *S. domesticus* is incorrect. All domestic pigs and their wild progenitor in any of its possible states of existence--wild, feral, pariah--should be given the same specific designation, *Sus scrofa*.

Differences among Domestic, Wild and Feral Pigs

Where the ranges of the wild boar and feral pig overlap or when wild boar breed with domestic or feral pigs, a variety of intergradations between the wild and domestic or feral pig can be found (Table 3). The differentiation of one form of pig from another may become desirable or even necessary for the law enforcement officers, forensic veterinarian, land manager, field biologist, or the trophy hunter. The ability to distinguish the domestic pig from its wild ancestor is also important for the zooarchaeologist. This section of the dissertation selectively reviews some of the more important differences among domestic, feral and wild pigs.

(a) Morphology

Physical characters in the wild boar and the domestic pig have been contrasted by Jones (1959), and Stegmen (1938). Compared to the domestic pig, the wild boar has a longer, more pointed head; smaller ears which are pointed and haired; is more streamlined in body; is higher at its shoulder region and has a well developed mane. The tail of the boar is mule-like and bears a tuft of hair distally. Males have thickened skin known as shields over their shoulders. The pelage

TABLE 3: Possible mating types among wild, domestic and feral pigs, and their expected karyotype frequencies.

Crosses		Expected karyotype frequency			Examples of studies on selected crosses
Type	Karyotype combination	36	37	38	
Wild pig x wild pig	36 x 36	1			Tikhonov & Troshina 1978; Troshina & Tikhonov 1980
Wild pig x cross-breed	36 x 37	1	1		Tikhonov & Troshina 1978; Troshina & Tikhonov 1980; Mauget 1981
Wild pig x domestic/feral pig	36 x 38		1		Zurowski *et al* 1970; Mahendranathan & Mellish 1971; Tikhonov & Troshina 1978; Townsend *et al* 1979; Troshina & Tikhonov 1980; Mauget 1981
Cross-breed x cross-breed	37 x 37	1	2	1	Tikhonov & Troshina 1978; Troshina & Tikhonov 1980; Mauget 1981
Cross-breed x domestic/feral pig	37 x 38		1	1	Troshina & Tikhonov 1980
Feral pig x feral pig	38 x 38			1	Barrett 1978

consists of coarse bristles and distinct dense winter undercoat of wool-like hair. In Asia, the wild boar changes its coat annually; the annual moult begins in spring and continues into summer (Sowerby 1930). Shedding of the boar's summer coat has also been reported in the United States (Henry 1969), and having been observed in feral pigs in South Carolina.

The normal coat color of adult boars varies from light to dark gray to black (Jones 1959; Henry 1969). Piglets are born with a longitudinally-striped coat pattern made up of six yellowish-brown stripes alternating with five black stripes (Diong 1973). Juvenile striping is a dominant trait (Zurowski et al. 1970) and is useful in distinguishing young of wild boar from those of domestic pigs. Juvenile striping has, however, been observed in feral pigs (Giffin 1978) as well as among domestic pigs in the Pacific (Malo 1951). Appearance of some semblance of the ancestral juvenile coat pattern in domestic and feral pigs may be explained by the past breeding history of the pigs or the reversion to wild type characters when domestic pigs become free-living.

In adult boars, the bristled hairs are split distally into two or more parts (Boback 1957; Jones 1959). Henry (1969) considered split guard hairs and juvenile coat pattern as two useful field methods for distinguishing the boar from either the domestic or feral pig. Springer (1977) used hair color, presence of mid-dorsal mane and distally-split guard hairs to distinguish wild boar from feral pigs. Singer (1981) listed, among other traits, juvenile striping, split guard hairs and presence of a mane as typical traits for the wild boar.

Contrary to claims by Bird (1955), Jones (1959) and Henry (1969), that split guard hairs are a useful criterion for distinguishing the boar from domestic or feral pigs, Kurz and Marchinton (1972), and Marchinton et al. (1974) observed that distally-split hairs are found in the boar, domestic and feral pigs. These authors concluded that the split guard hairs character alone is of no use in distinguishing pigs in their various states of existence.

In habitats where wild boar interbreed with feral or domestic pigs, use of coat color alone to differentiate one form of pig from another may be problematic. Domestic-type coat color patterns such as brown, white or piebald may appear in the different mating types. These domestic-type coat colors have been mentioned by Jones (1959), but are more lucidly illustrated by Meynhardt (1978) and Mauget (1981).

(b) Cytogenetics

Counts of somatic chromosomes are useful to distinguish the boar from domestic or feral pigs. Barrett (1971, 1978) showed, by karyological studies, that variously colored feral pigs in the Sierra foothills of California had diploid chromosome counts identical to that for domestic pigs, i.e., $2n=38$, whereas the introduced wild boar had a diploid chromosome count of $2n=36$. Giffin (1977, 1978) observed that feral pigs on Mauna Kea, Hawaii, had domestic karyotypes, $2n=38$, despite the fact that the pigs he sampled were all phenotypically similar to the European wild boar. Wood and Barrett (1980) believed cytogenetic determination to be the most reliable method currently available for establishing the identity of a pig population, especially in areas where the boar and feral pigs occur together.

Karyotypes in the wild pig have some peculiarities, whereas domestic pigs, regardless of their breed type or geographic locations, have a stable karyotype of 2n=38 (McConnell et al. 1963; Stone 1963). The wild boar exhibits intrapopulation karyotype polymorphism (Tikhonov & Troshina 1978; Troshina & Tikhonov 1980). Karyotypes 2n=36 and 2n=37 have been reported for wild boar populations in Tennessee (McFee et al. 1966; Rary et al. 1968), Germany (Grop et al. 1969) and karyotype 2n=38 has been reported for four populations of wild boar in Yugoslavia (Zivkovic et al. 1971) and for the wild boar in Japan (Muramoto et al. 1965). Wild boar karyotype 2n=36 differs from that in domestic pigs by possession of one extra pair of submetacentric chromosome, while lacking in two pairs of telocentric chromosomes; the "extra" submetacentric chromosome in the boar and the "extra" telocentric chromosome in the domestic pig are homologous and involved in Robertsonian translocation (Bosma 1976). Karyotype 2n=37 in the boar has been explained as the result of entry of the domestic genome into a wild population (McFee et al. 1966) or from feral pig wild boar crosses. Karyotype 2n=37 has one extra submetacentric chromosome and two unpaired telocentrics, which are absent in karyotype 2n=36 but belonging to the two pairs of telocentrics in domestic pigs (Bosma 1976; Mauget 1981).

Two hypotheses have been advanced by Bosma (1976), and Troshina and Tikhonov (1980), to explain how domestication could result in karyotype transformation: [1] The domestication process transforms the ancestral karyotype 2n=36 to 2n=38 in the domesticant. The increase in chromosome number is brought about by the centric fission of one pair of submetacentric chromosome, thus producing two pairs of telocentrics. [2] The original boar karyotype was 2n=38. This evolutionarily more primitive karyotype is retained in domestic pigs, but has decreased from 2n=38 to 2n=36 in modern-day European wild pigs. The reduction in chromosome number is brought about by the centric fusion of two pairs of telocentric into one pair of submetacentric chromosome. Chromosome number reduction and the appearance of polymorphism in wild boar is therefore thought to be a recent event.

In the continental United States, wild boar are known to interbreed with feral pigs (Pine & Gerdes 1973; Barrett 1977; Smith et al. 1980; Singer 1981). In Europe, domestic pigs are known to breed with the wild boar (Zurowski et al. 1970; Meynhardt 1980). In Malaysia, the east Asiatic wild boar has been observed to breed with domestic pigs in jungle fringes (Mahendranathan & Mellish 1971). With interbreeding, various types of crosses are possible (Table 3). Interbreeding introduces domestic type color variation and other morphological variations into the wild population. Physical characters alone are not always useful in accurately distinguishing one form of pig from another.

(c) Anatomy

(i) Teeth.—Domestication results in the shortening of the pig's cranium (Zeuner 1963), followed by size reduction of cheek teeth and the length of the tooth row. Among the several characters used by archaeologists to differentiate domestic from the wild pig, absolute size of the molars has proved most reliable (Reed 1961). Tooth row length, but especially length of the second and third molars, are shorter in domestic than in wild pigs.

(ii) Bones.—Popovic (1977) compared whole skeletons of the boar with that of domestic pigs for morphological properties. He observed that bones of wild boar and domestic pigs are very similar, but there are some significant differences. In the boar the spinal vertebrae are relatively shorter (hence a shorter spinal column), but the spinal processes of the cervical, thoracic, and lumbar vertebrae are considerably longer and narrower when contrasted with those in domestic pigs. The width difference between the spinal processes at the distal and proximal ends is more marked in wild boar than in domestic pigs. Bones in the anterior limb humerus and scapula are markedly longer and thinner in the boar, whereas bones in the hind extremities, especially the pelvis, are markedly longer and narrower in the boar than in domestic pigs. It should be pointed out that Popovic's (1977) conclusions were made from a study of whole skeletons of five wild boar and ten domestic pigs.

(iii) Kidneys.—There are several structural and functional differences between the kidneys of wild boar and domestic pigs (Thiessen 1976). Kidney cortex and nuclei are smaller in the boar, but oxygen consumption in boar kidney tissues is higher than in kidneys of domestic pigs. Kidneys of domestic pigs have more fat. Crossbreeds from wild boar and domestic pig crosses have significantly higher kidney fat weight which is thought to be the result of genetic contribution from domestic pigs (Mahendranathan & Mellish 1971). Boar kidneys have a higher concentration of amino-acids in the medulla. LDH and NADP activities are higher in the boar. Thiessen (1976) suggested that this might be due to increased production of lactic acid and alpha-ketoglutaric acid for energy metabolism whereas domestic pigs probably use more fatty acid.

(iv) Central nervous system.—The brains of wild, domestic, and feral pigs have been well investigated by several European workers (Rohrs & Kruska 1969; Kruska & Stephan 1973; Kruska & Rohrs 1974; Hadziselimovic & Dilberovic 1977; Guntherschulze 1978). Domestication reduces the brain size and brings about qualitative changes in the brain structures. In the domestic pig, brain size is 34% smaller than in the boar; the telencephalon is more reduced than the other parts of the brain (Rohrs & Kruska 1969). Olfactory structures in domestic pigs are 28% to 32% smaller than wild boar of comparable body weight. Reduction in the olfactory areas in domestic pigs is reflected in the smaller size of the regio olfactoria whose olfactory area is 43% smaller than those in the boar. The wild boar has the largest olfactory area among mammals and adult wild pigs have 1.5 times more olfactory receptors than do domestic pigs (Guntherschulze 1979). Even more remarkable is the size difference in limbic structures such as the hippocampus and schizocortex which are 40-43% smaller in domestic pigs (Kruska & Stephan 1973). Brain size reduction consequent to domestication has been attributed by the above authors and also by Kruska (1980) to intraspecific adaptations to domestication, different rates of evolution, effects of selection regimes imposed by man and behavioral changes in unstressed environments.

Comparative-qualitative studies in brain size and structure in feral pigs in the Galapagos Islands and European domestic pigs by Kruska and Rohrs (1974) revealed some interesting similarities and differences. The brain size of feral pigs is identical to that in domestic pigs suggesting that feralization cannot reverse the brain size reduction produced by the domestication process. However, the diencephalon and medulla oblongata in feral pigs are respectively 6.5% and 10% larger than those in domestic pigs, and the cerebellum, on the contrary and somewhat inexplicably, is 11% smaller than in domestic pigs. The total limbic structures are 17% larger and the hippocampus is 25% larger when compared to domestic pigs. The telencephalon in feral pigs is about the same size as in domestic pigs, but the allocortex is 11% larger in feral pigs. The bulbus olfactorius in feral pigs is 28% larger than in domestic pigs, although olfactory bulb size in feral pigs does not differ from those in wild boar. It should be pointed out Kruska and Rohrs' (1974) observations were drawn from an insular population of feral pigs with a feral history of 70 to 140 years.

(d) Behavior

Large behavioral differences exist between domestic pigs and the wild boar. In domestic pigs, the group structure characteristics of wild pigs has disappeared, the activity levels have decreased, escape behavior is weak, escape distance is smaller (Grzimek 1976) and nest building behavior is less elaborate. Aggressive and predatory behavior are less developed, in part due to the smaller hippocampus formation (Kruska & Rohrs 1974). Behavior in feral pigs resembles more that of the wild ancestor than of domestic pigs. Differences in behavior among wild, domestic, and feral pigs may be explained by the quantitative and qualitative changes in the brain following domestication or return to free-state existence. Feral pigs are less sedentary and more mobile than wild pigs as indicated by the larger medulla oblongata (Kruska & Rohrs 1974). The larger diencephalon in feral pigs indicates that acoustic and visual centers are more important for feral pigs than for domestic pigs. Thus the sense of smell, food search behavior, orientation, individual recognition and mate finding are more strongly developed in wild and feral pigs than in domestic pigs. Despite identical brain size in feral and domestic pigs, the larger hippocampus in feral pigs suggests that feral pigs, under the regime of natural selection, have higher activity functions, higher levels of alertness and are more aggressive than domestic pigs.

(e) Biology

Wild boar generally litter once a year, but the second litter when produced is usually smaller than the first (Boback 1957). In contrast feral pigs breed all year round, although farrowing peaks have been observed (Barrett 1978; Giffin 1978). In Eurasia wild pigs conceive at about 17 months, whereas feral pigs conceive at six to 12 months; the typical fetal rate is 4.4 to 5.6 for the wild boar and 5.4 to 5.8 for feral pigs (Singer 1979). The wild boar is migratory, but this behavior has not been observed in feral pigs. Published densities range from 0.04 to 60 pigs per km^2 for the boar and from 3.9 to 115 pigs per km^2 for feral populations (Barrett 1978; Singer 1979).

Introduction of the Pig into the Hawaiian Archipelago

(a) Geographic origin of the Polynesian pig

In this dissertation, the term Polynesian pig is applied to the aboriginal pig that was introduced into the Pacific islands by migrating Polynesians during prehistoric times. Used as defined here, the Polynesian pig is therefore free from any influence of domestic breeds introduced into the region following European contact.

The origin of the Polynesian pig is generally traced to Melanesia, Indonesia or South-east Asia (Handy & Handy 1972) but the ancestral subspecies from which the small Polynesian pig is derived has not been answered in a definitive way. Several methods are available to investigate affinities among geographic races of pigs. Comparative taxonomic studies on skeletal structures of the aboriginal pig and subspecies in the South-east Asia and South Sea islands would help trace the origin of the Polynesian pig and establish its affinity with other races. This taxonomic approach requires comparison of large samples of the aboriginal pig from throughout Polynesia, Melanesia and Micronesia for comparative studies with those samples in the Sunda and South-east Asian regions. No such collection exists. To the early explorers in the Pacific, the pig was unquestionably a valuable and most esteemed, but all too common and readily available exotic food animal. Not surprisingly, collections made by Captain Cook and other explorers and naturalists contained no specimen of the aboriginal pig. Modern immunogenetic studies, similar to the ones conducted by Kurosawa et al.

(1979) are extremely promising in providing definitive answers on the evolutionary and phylogenetic relationships of the aboriginal pig to the geographic races in the South-east Asian mainland, Sunda islands, and Pacific region. Immunogenetic studies would require genetically pure aboriginal Polynesian pigs for tissue sampling. Unfortunately, such pure Polynesian stock can no longer be found or established with certainty. Therefore investigative methods discussed above have only limited applications.

Notwithstanding the aforementioned difficulties, there have been previous attempts to answer the two frequently recurring questions on the Polynesian pig: [1] What was its origin? [2] How can it be described? Warner (1959) searched major zoological references in an attempt to trace the origin of the Polynesian pig, but having obtained no new information, concluded that the Polynesian pig could be considered a subspecies of the European wild boar, <u>Sus scrofa</u>. Titcomb (1978) attempted a literature search on the Polynesian pig, but observed that little has been published on the pig. In contrast, Bellwood (1980) lucidly reports that among the animals in the Polynesian triad--pig, dog and fowl--more is known about the pig than the other two animals; though much of the information is anthropological and of circumstantial nature. Although it is true that no scientific text or references exist specifically concerning the Polynesian pig, the literature search conducted in this study reveals extensive information on the aboriginal pig but these are scattered about in obscure non-zoological references. Only the most pertinent and less controversial papers are cited in this dissertation. Urban (1961) gives, by far, the most comprehensive and in-depth treatment on the pig and the other two animals in the Polynesian triad.

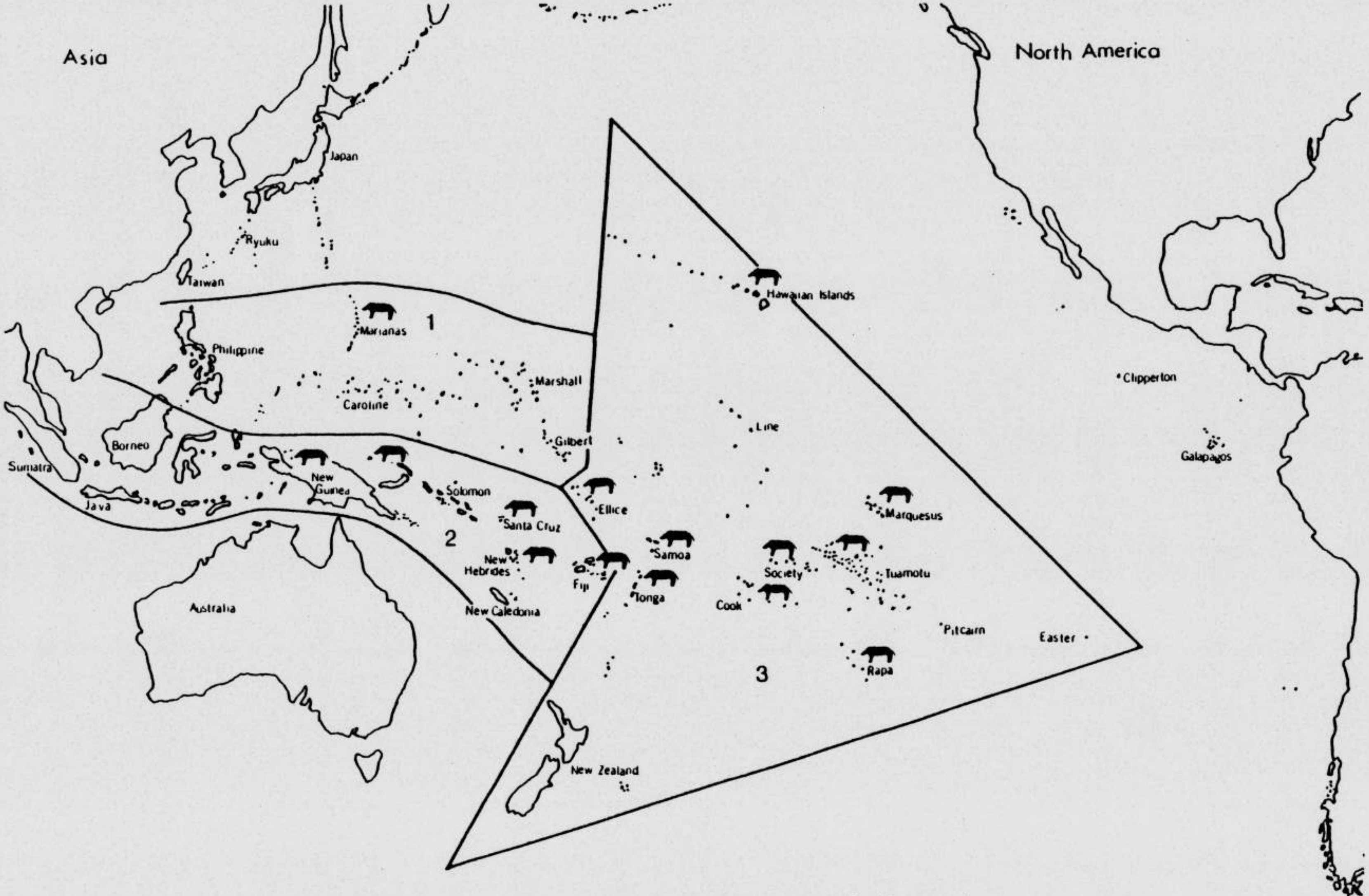
In what follows an attempt is made to trace the origin of the Polynesian pig by examining three factors.

(i) The history of pig domestication.--The domestication centers for the pig, starting from the earliest times to the most recent may be ordered as follows: South-west Asia, Europe, Near East, China and South-east Asia. In the late Neolithic era, and by about 3000 B.C., the pig was already domesticated in South-east Asia. Movements of humans eastwards into Oceania began at about the same time the pig was domesticated (Bellwood 1980). Zooarchaeological studies show that the pig was already introduced into New Guinea by about 3000 B.C., indicating therefore that the pig was moved eastward in its early phase of domestication. Interestingly, the movement of migrants eastward from the South-east Asian mainland occurred with the domestication of the pig and this, according to Bellwood is not coincidental. The introduction of pigs beyond New Guinea into the Pacific took place after 1500 B.C. (Bellwood 1980). That the pigs in the Pacific originated from South-east Asia has been further supported by findings that internal parasites of pigs in the Pacific are of Asiatic origin (British Admirality 1945).

(ii) The prehistoric migratory routes of the Polynesians from their points of origin into various major island groups in Oceania.--The pattern of Polynesian settlement as reconstructed by Sinoto (1968) is shown (slightly modified) by the arrows in Figure 2. Two migratory routes have been established. The Melanesian route originated in the Indo-Malayan region, was more frequently used and was associated with the following major island groups--Sumatra, Java, other Indonesian islands, Malaysia, Borneo, New Guinea, Solomon islands, New Hebrides and Fiji. The Micronesian route is believed to originate from Southern China and the Philippines. Both routes lead into the Marquesas, which, according to Sinoto (1968), were the primary dispersal center in Polynesia. Settlement pattern into the Hawaiian islands began between 600 to 1000 A.D., first via the Marquesas and later from Tahiti and the Society Islands. It was along these migratory routes that the Polynesian pig was transported from one island group to another.

(iii) The indigenous distribution of pigs in South-east Asian Mainland, Indonesia and the Sunda Islands.--Mainland Southeast Asia and the Indo-Malayan region, origins of the Melanesian migratory route, were represented by four indigenous pigs of which three were Sus species, S. scrofa, S. verrucossus, and S. barbatus, and the fourth B. babyroussa (Table 1). The last three species mentioned possess distinct species characteristics which differ from those of S. scrofa (Table 2), have never been domesticated, were never mentioned or described by any explorer in the Pacific, and have not, to date, been found in archaeological excavations in the Pacific region.

Figure 2: Distribution of the aboriginal Polynesian pig in Oceania during preEuropean era. Note that the pig was noticeably absent in Australia, New Zealand and several island groups. Migratory routes (1, 2) for the early settlers and the aboriginal pig are indicated as Micronesian or Melanesian route. See text for details.



1 Micronesian route 2 Melanesian route 3 Polynesia

By the process of elimination, it must be concluded that the early domestic pig, that is, the Polynesian pig, that was transported eastwards was derived from *S. scrofa*. This species is represented in the Southeast Asian region by at least ten subspecies (Table 1). However, because of the rather distinct size and body characters of the Polynesian pig which differ from those in modern domestic breeds, a further question could be asked: What is the most probable ancestral race of *S. scrofa* from which the Polynesian pig was derived?

Currently, there are two schools of thought with regard to the origin of the aboriginal Polynesian pig--one believes *S. s. papuensis* (Lesson & Garnot 1826) to be the ancestral species whilst the other is of the opinion that *S. s. vittatus* (Boie 1828) was the ancestral race from which the aboriginal pig was derived. Both schools of thought are evaluated below.

S. s. papuensis, also known as the "Papuan or New Guinea pig" was widely distributed throughout New Guinea, the Admiralty Islands, Bismarck Archipelago, the Solomon Islands, Yap, Ceram, the New Hebrides, other parts of Melanesia and other Pacific islands (Haltenorth 1963). Although Murray (1866), Haltenorth (1963), Heptner et al. (1966), and Haber (1969) included New Guinea as the native range for *Sus scrofa*, Laurie and Hill (1954) observed that pigs of the *scrofa* group found in New Guinea, Bismark and Louisiale Archipelago, Solomon Islands and Melanesia were feral descendents carried from island to island by human agency. Mauget's 1981 map on native distribution of *Sus scrofa* does not include New Guinea as the range for *S. scrofa*. According to Vayda

(1972), pigs in New Guinea originate from those introduced prehistorically and from recent European introductions.

The transport of domesticated pigs eastwards beyond New Guinea occurred after 1500 B.C., and it is thought quite presumptuously that *S. s. papuensis* was carried along the Melanesian migratory route into central Polynesia and then into the Hawaiian Archipelago. Heyerdahl (1952) points to the similarity (considered erroneous in the present evaluation), between the Polynesian pig and *S. papuensis* (sic) and suggested that the aboriginal Polynesan pig introduced into the Hawaiian islands was derived from *S. s. papuensis*. Based on available information that can be drawn from the literature, the *papuensis* hypothesis is refuted here for the following reasons:

[1] Examinations of early illustrations on *S. s. papuensis* by Freycinet (in Jardine 1836 Vol. 5 plate 19), and other illustrations on early pigs in the Pacific (Table 4) showed that *S. s. papuensis* was not represented in Polynesia, in the illustrations examined, at least. None of the Polynesian illustrations resemble *S. s. papuensis*. Choris' (1822) illustration entitled "Port d'Hanarourou" depicts two pigs whose profile may superficially appear to resemble that of *S. s. papuensis*, but the features of the body of the two pigs do not resemble those of *papuensis*.

[2] The descriptions by Cook (1784), Ellis (1831), and Bennett (1840) for the typical aboriginal Polynesian pig of the Pacific bear no resemblance to, and differ considerably from, the original description

TABLE 4 : List of 17th-18th Century illustrations of pigs in Hawaii and the Pacific area, as seen by artists, explorers and naturalists.

Year	Artist/ Author	Title of painting/illustration	No. of pigs in painting/ illustration	References
1768-1771	Webber	A view of Anamooka	1†	BMNH; ADD MS 23920 f 94
1768-1771	Webber	A morai with an offering to the dead	1	BMNH; ADD MS 23921 f 28
1768-1771	Webber	An island view in Atooi	1†	BMNH; ADD MS 23921 f 68
1768-1771	Webber	An offering before Captain Cook in the Sandwich islands	2	BMNH; ADD MS 23921 f 75
1768-1771	Webber	A human sacrifice at a morai in Otaheite	4‡	BMNH; ADD MS 23921 f 30*
1768-1771	Webber	A bay scene	1†	BMNH; ADD MS 15513 43.613.65
1768-1771	Webber	Untitled (Two men carrying a pig)	1†	BMNH; ADD MS 15513 43.613.67
1778	Hodges	A view in the island of Rotterdam	1†	BMNH; ADD MS 23920 f 93
1794	Heddington	Village of Macacoupah, Owhyee	3†	BPBM; Negative #23684
1816	Choris	Port d'Hanarourou, in Voyage Pictoresque (1822), plate #18	2†	BPBM; Negative #20582
1816	Choris	Temple du Roi dans la baie Tiritatea, Ahuena heiau, Kailua, Hawaii	1	BPBM; Negative #20569
1820	Choris	A Hawaiian scene	1†	BPBM; Negative #20599
1826	Lesson	Papuaschwein (Sus papuensis) mit Schadelskelett, Neuguinea	1†	Lesson, P.A. (1826), Histoire Naturalle, Zoologie Tafel 8
1828	Frecynet	Papuan hog	2†	Jardine, W.B. (1836), plate #19
1853	Mettais & Bocourt	Canards et cochons (ile Taiti)	2†	Montemont (1853), Jacques Cook, p.32
1924	Pritzwald	Sus vittatus	1†	Pritzwald, S. (1924), Figure 59

BMNH = British Museum Natural History, London, England

BPBM = Bernice P. Bishop Museum, Honolulu, Hawaii

† live animals

* also in Bernice P. Bishop Museum, Honolulu, Negative #19318

‡ see Luomala (1962) for arguments that two other animals in illustration were dogs and not pigs.

of the *S. s. papuensis* by Lesson and Garnot (1826). *Sus s. papuensis* has four pairs of nipples, very short tail, poorly developed canines, shorter ears, but longer body in relation to its head, saddled back, wrinkled skin with its coat color predominantly reddish-brown and its abdomen whitish in color (Lesson & Garnot 1826). No pig with this description was ever recorded by any explorer or naturalist for the Pacific region. Observing the peculiar features of *S. s. papuensis* and the variability of pigs in the South Sea islands, Lesson and Garnot (1826) made no reference to *S. s. papuensis* as a probable ancestor of the Polynesian pig.

S. s. vittatus (Boie 1828) (synonym: *vittatus* Muller & Schlegel 1842) had a native range in Mainland Southeast Asia, Indonesia and Sunda islands to Timor, but was also transported into New Guinea (Zeuner 1963). Known as the Sunda wild pig (Zeuner 1963; Haltenorth 1968) but more commonly as the East Asiatic wild boar, *S. s. vittatus* was widely distributed at all points of origin of the Polynesian migratory routes. It is today considered to be the ancestral race from which Asiatic domestic pigs are derived (Fradrich 1972; Ensminger 1977; Pond & Houpt 1978). According to Pritzwald in Urban (1961), it was the domesticated form of *S. s. vittatus* that was introduced prehistorically into the Polynesian islands. Urban (1961) reviewed the works of several German workers, which all point to *S. s. vittatus* as the origin of the South Sea pig. Hence it may be concluded that while other domestic races may have been transported into Polynesia, *S. s. vittatus* is the most probable ancestor to the aboriginal Polynesian pig.

Having reviewed the possible origins of the Polynesian pig in the Pacific, a related question could be asked: In what state of its existence was the pig transported into Polynesia? Transport of pigs other than domestic ones seems possible, but extremely unlikely. From the journals of Captain Cook, it is observed that pigs do not make good sea passengers. They became sea-sick easily, were susceptible to cold, die at sea, had to be supplied with an agreeable ration of vegetables or coconuts with which they were normally fed (Cook 1784 Vol. I pp. 139-140, 151) and were noisy animals (Luomala 1975). Domestic pigs would be easier to manage than non-domesticated ones in the double-hull canoes, and ensured a sustained supply of meat-on-the-hoof. Additionally, archaeological excavations at sites along the migratory routes have only yielded bones of domesticated pigs (Bellwood 1980). The aboriginal Polynesian pig therefore had no wild ancestor in the Pacific, it being derived from the East Asiatic boar S. s. vittatus, and was transported during its early phase of domestication, eastwards into Oceania.

(b) Description of the Polynesian pig

This section reviews the history of the Polynesian pig, answers the question on the profile of this pig and explains why the seemingly striking species characteristics in the aboriginal pig were early type domestic traits.

The pure aboriginal Polynesian pig had been well described by several Pacific explorers, whalers and missionaries (contra Warner 1959;

Titcomb 1978). However, no mention was made of the race or subspecific designation of this pre-European pig. Two observations may be made on this pig:

[1] The aboriginal Polynesian pig was the predominant domestic pig seen on all the islands visited by the early explorers. Because of its wide distribution in the Pacific, explorers had at various times called the Polynesian pig the "Southsea pig" (Cook 1784; Lesson & Garnot 1826; Bennett 1840), "the island pig" or "the pig of the indigenous people" (Urban 1961). Cook (1784) reported that the domestic Polynesian pig he observed on Kauai, Hawaii were of the same kind he had encountered in the South Pacific islands (Cook 1784, Vol. II p. 228).

[2] The Polynesian pig was already well distributed throughout Polynesia at the time of European contact (Figure 2). Its pattern of distribution among island groups in Oceania was, however, quite irregular (Sharp 1963; Urban 1961; Bellwood 1980) as a number of Polynesian islands suited to the pig did not have it (for complete list of individual islands see Cook 1784 especially Vol. II, British Admirality 1943, 1944, 1945a,b; Urban 1961; Sharp 1963; Luomala 1975; and Bellwood 1980). The Maoris, for example had the dog and rats, but not the pig. Pigs were, however, not found in New Zealand, Easter Islands, Niue, Mangaie, Aitutaki and the Gilbert islands (Figure 2).

For the purpose of this dissertation early descriptions of the Polynesian pig were drawn from an explorer, Captain Cook; a missionary, W. Ellis; and a whaler, W. Bennett. Cook (1784) described the aboriginal Polynesian pig in the Hawaiian islands as "a small species of hogs with long erect ears" (Cook 1784, Vol.II p. 228). When Cook discovered Maui, the natives brought him "small pigs" (Cook 1784, Vol. II p. 531). On the island of Hawaii, Cook commented that he could seldom get a pig over 50 or 60 pounds (Cook 1784, Vol II p. 544). Writing on the natural history of the Hawaiian Islands, Ellis (1831) described the original pre-European contact pig as "...a small species of hogs, with long heads and small erect ears..." (Ellis 1831, Vol. 4 p. 24). In the Society Islands, Ellis recorded his observations on the Polynesian pig as an animal "...with long legs, long noses, curly or almost wooly hair and short erect ears...and the people say such were the only hogs formerly in Tahiti..." (Ellis 1831, Vol. 1 p. 324). By far the clearest and most detailed description of the Polynesian pig was that by Bennett (1840, Vol. 1 p. 342) who described the aboriginal pig of Tahuata, Marquesas as follows:

> "...the hogs still exhibit, in great purity, the gaunt form, acute snout, arched back, high tail, pricked ears, and small deer-like feet, of the aboriginal Polynesian breed. Their prevailing colour is black; their bristles are long and shaggy, and the skin beneath has a thick covering of short crisped hairs, closely resembling wool. The old boars have tusks of vast size..."

To summarize, it can be seen that the Polynesian pig was characterized by the following features, (1) relatively small size, (2) long snout, with short erect ears, (3) predominantly black coat with bristled hairs and woolly undercoat, (4) arched back, high tail, deer-like feet with long legs, and (5) juvenile striping present in the young. All the described features and known behavior (see Ellis 1831, Vol. 1 pp. 70-71) of the aboriginal pig are neither found in modern domestic breeds nor in imported European domestic pigs. The described characters were closer to the wild ancestor. Yet the Polynesian pig was undoubtedly a domesticated animal. This manifestation of ancestral characters in the Polynesian pig may be explained by examining its domestication history. It is apparent that the aboriginal Polynesian pig and the imported European domestic pig had two contrastingly different domestication histories. With European contact in the Pacific established in 1513, it follows that the domestication history for the imported domestic pigs at the time of first European contact was at least 8500 years, whereas that of the Polynesian pig was about 4500 years. Hence the Polynesian pig lags behind the European breeds by a domestication history of at least 4000 years. It was therefore in a relatively early phase of its domestication process.

Assuming that the modification from wild to domestic characters is a linear function of time, then it can be inferred that more of the ancestral characters, and hence less of the domestic characters, would be seen in early domesticants, as is the case in the Polynesian pig.

Animals in their early phase of domestication tend to be smaller than their wild ancestor. Zeuner (1963) discussed the changes following domestication and the traits characteristic of domesticated forms. These have been summarized by Berry (1969). That the Polynesian pig is a relatively small animal is suggestive of its early domesticity. The insular environment may have, in addition, contributed to the selection of a smaller animal. In general, pigs appear to increase in size from the west to the east, with continental forms growing larger than those living on islands. On Kangaroo island, Australia, feral pigs with an insular history of 180 years have evolved into a new racial type approaching the size of miniature pigs (McIntosh & Pointon 1981). Smaller size may also be due to inbreeding (Ensminger 1977) or to the effects of a lower nutritional plane experienced over generations. Another important effect of domestication is the shortening of the facial parts of the skull relative to the cranium (Zeuner 1963). The long snout in the Polynesian pig, indicative of its unshortened ancestral cranium, again shows that the aboriginal pig is an early domesticant. Other characters in the Polynesian pig, which according to the works of Zeuner (1963), would be indicative of an early type of domesticated animal are black bristled hairs with woolly undercoat, large canine teeth, and juvenile coat striping. Thus it can be seen that the Polynesian pig transported eastward into Oceania was in its early domestication history. The description of the pig therefore provides an idea of what the profile of a domestic pig, probably derived from S. s. vittatus, would look like during its early phase of domestication.

To further describe the pig, an attempt was made at locating early illustrations that might contain sketches of the Polynesian pig. Microfilms on Webber's paintings during Cook's voyages to the Pacific between 1768-1771 (Microfilm No. 3821, British Museum Natural History, London) were examined together with high contrast black and white prints supplied on request by the British Museum at Bloomsbury, England (Goode 1981 - pers. comm.; Barber 1981 - pers. comm.). In addition, a cover-to-cover search was conducted on most of the photoalbums at the Photocollection Library, Bishop Museum, Honolulu. A compilation of illustrations examined and found to contain sketches on early Pacific pigs and considered relevant to this review are listed in Table 4. The following conclusions are made from careful examination of exhibits contained in Table 4:

[1] None of the illustrations contain representations on the aboriginal Polynesian pig. Hogdes' drawing entitled "A view in the island of Rotterdam" (folio 93, MS 23, 920, British Museum at Bloomsbury) is the only illustration of a pig depicting some characters of the Polynesian pig. The Tongan island pig in Hodges' illustration was black and bristled, arched back, had a long hanging tail which would have been straight except for a kink at about mid length, had relatively small erect ears which were pointed backwards, and was more ancestral in appearance than any other illustrations examined.

[2] There was considerable variability in the appearance of the pigs; this morphological variation may be attributed to interbreeding of the aboriginal breed with Spanish, English and Asiatic breeds, as pointed out by Cook 1784.

[3] Domestic-type characters were evident in most of the illustrations, with the exception of the pig in Hodges' (ibid).

Domestic characters observed were (i) piebaldness, for example, Webber's illustration on "A view of Anamooka." Piebaldness may result from mutation of black coat color in the wild ancestor to white and patchy coat colors (Andrezejewski et al. 1975) or from interbreeding. Zeuner (1963) considers piebaldness as an evidence of domesticity. (ii) Curly tail, for example, in Choris' sketch on "A Hawaiian scene." (iii) Large hanging ears, for example, Mettais and Bocourt representations on "Canards et cochons (ile Taiti)." Luomala (1962), on examining Webber's scene, "A Human Sacrifice in a Morai, in Otaheite" repeatedly made mention of the "long-eared" character of the pig in Webber's illustration and suggested that the long-eared pig may be a "native pig," (sic), that is, the Polynesian pig. But Webber's illustration was that of a singed pig. My field experience in Kipahulu Valley demonstrated that singing has the effect of transforming domestic type hanging, flappy ears to firm, erect ears which also appear more pointed and directed backwards.

Loss in identity of the Polynesian pig through interbreeding with other imported domestic breeds must have begun as early as 1513. From the time of first European contact to about the time of Captain Cook, the predominant breed in the Pacific was the Polynesian pig. Submergence of the aboriginal breed may have been accelerated by imported breeds (Urban 1961). The transition in the disappearance of the aboriginal pig from its pure breed to its mixed breed condition has been described as "rapid" by early explorers and missionaries. In the Society Islands Ellis (1831) wrote that the aboriginal Polynesian pig "is now and then seen" (Ellis 1831, Vol. I p. 70), but added that, in general, pigs on the islands were "a mixture of English and Spanish" (Ellis 1831, Vol. I p. 70). At about the same time, Bennett (1840) observed that "the hog still (emphasis is mine) exhibit a great purity" of aboriginal breed in the Marquesas, but his observations on the loss in identity of the Polynesian pig in the Society Islands were similar to, but even more graphic than, those of Ellis' (1831). He described the submergence of the characters of the aboriginal breed as follows:

> "...Swine are excellent, but in the present mixed breed, impossible to detect any trace of the aboriginal hog of Polynesia. The pricked ears of the latter animal have in almost every instance given place to the broad and pendant ears, the badge of slavery..."
>
> (Bennett 1840, Vol. I p. 86)

One observed consequence of interbreeding was the improvement in the size and weight of the aboriginal pig. On the Society Islands, Cook (1784) observed that "the hogs are of a large kind, have already greatly improved the breed originally found by us upon the islands; and at the time of our late arrival were very numerous..." (Cook 1784, Vol. II p. 75). For Hawaii, Kotzebue (1821) observed that "the hogs are so large that the whole crew could not eat one in two days..." (Kotzebue 1830, Vol. 1 p. 327). Quite understandably, explorers, sailors and natives alike welcomed and even encouraged the crossing of the aboriginal pig with imported European and Asiatic breeds. In 1777, Cook (1784) landed "...an English boar and sow...so that not only Otaheite, but all the neighbouring islands will, in a few years, have their race of hogs considerably improved..." (Cook 1784, Vol. II p. 134).

It should be borne in mind that imported European pigs were already a considerably improved domestic breed because of previous crossing with Chinese and other Asiatic domestic pigs which were known for their higher fecundity (Mellen 1952; Fradrich 1972). The influence of Asiatic breeds in submerging the Polynesian pig may have come from direct importation of Asiatic breeds eastwards into Polynesia. Forster's (1826) description of a pig from the South Sea islands as "the Chinese variety with short legs, a stomach that hangs to the floor and body with scanty hairs..." suggests direct importation of east Asiatic domestic breed into Polynesia. A good review of domestic breeds of Asiatic Chinese pigs has been given by Phillip and Hsu (1944). Pig importation was an intense activity in the 1800s during the days of the sealers, traders, whalers, missionaries and settlers. The identity of the Polynesian pig was considered lost by the early 1900s (Urban 1961). For the Mangareva Group, the British Admirality (1945, Vol. II p. 231) reported "...while their own domestic pig (that is, the Polynesian pig) became extinct...the ordinary European domestic animals are now there in small numbers..."

To recapitulate and to summarize, the following may be said about the Polynesian pig in Oceania:

[1] the Polynesian pig probably derived from S. s. vittatus, was transported by early migrants throughout Southeast Asian islands, Sunda Islands, and eastwards into Polynesia;

[2] the aboriginal pig that was transported into Polynesia was separated from European breeds by a domestication history at least 4000 years shorter. It was in an early stage of domestication as evidenced by ancestral characters such as the longer snout, bristled black coat with an underwool, short, erect and pointed ears, arched back and straight tail; and,

[3] the history of the Polynesian pig may be divided into the following phases:

(a) prehistoric (pre-European) era, from about 1500 B.C. to 1513 A.D. During this era, the pure aboriginal breed had a wide but irregular distribution.

(b) post-European to pre-Cook era, from about 1513 to 1778. This period marked the transition of the aboriginal pig to European-type breed through interbreeding with imported Spanish, English, French and Asiatic pigs.

(c) post-Cook-missionary era, from about 1778 to 1850. This period saw increased sea-traffic and provisioning of ships with live cargo gain importance. Natives and immigrants welcomed and encouraged the improvement of the small bred Polynesian pig by crossing it with imported breeds. This era saw the rapid loss in identity of the aboriginal breed.

(d) postmissionary era to early 1900s. The identity of the aboriginal breed continued to be submerged and is believed to have been lost by the early 1900s. Thus, it can be seen that the aboriginal Polynesian pig had a history of about 3000-3400 years in Oceania.

(c) History of the feral pig in the Hawaiian islands

(i) Introduction and distribution.—Pigs have a longer history in the Hawaiian islands than in the continental United States. There were two stages of introduction, both involving domestic breeds. The Polynesian breed came in with island settlers during prehistoric times. Subsequently, Captain Cook became the first modern man to introduce European breeds on February 1, 1778, when he landed "a boar and a sow of English breed" on Niihau, and not on Kauai as recorded by Bryan (1937) and Kramer (1971). Cook who "had wanted to leave these (pigs, ram-goat, two ewes, melon seeds, pumpkins, and onions) at Atooi (Kauai)..." made his introductions into "Oneeheow island" (Niihau) instead (Cook 1784, Vol. II p. 217). The identity of the English breed was certainly lost through crossing with the natives' pig. Many importations of various domestic breeds were made by traders, whalers, sailors and ranchers during the postdiscovery era. At the time of his discovery, Cook observed that pigs were abundant, formed an important part of the natives' culture, and "were sometimes found wild in the mountains."

Today feral populations are found on all of the six major islands. Tomich (1969) and Kramer (1971) have reviewed their past and present distribution. Pigs are found in all types of habitat, with the densest populations in D1, D2, E1 and E2 vegetation zones of Ripperton and Hosaka (1942) (Kramer 1971). They are absent only in alpine stone deserts, barren lava flows and cinder fields (Warshauer 1980).

(ii) Forest pig versus mountain pigs.—Nichols (1962) recognized two varieties of pigs in Hawaii--the "mountain pig" and the "forest pig." The "mountain pig" on the island of Hawaii occurs in the more isolated and higher elevations on Mauna Kea and Mauna Loa, is a predominantly black bristled animal with a woolly undercoat, is more streamlined and has pointed ears, long legs and shoulder shields (Giffin 1977, 1978). This variety is also sometimes referred to as "razorback" and has been reportedly observed on Maui (Oliveira 1979 Nahiku, Maui - pers. comm.) in the early 1900s. The "mountain pig" on Kauai has a long straight tail and other features similar to the "mountain pig" on the island of Hawaii (Giffin 1977, 1978) and has been seen at lower elevations in kiawe (Prosopis) flats, and near sugar cane fields (Swedberg 1963). "Mountain pigs," variously referred to as "Hawaiian wild boar" or "Hawaiian pigs" (Swedberg 1963; Giffin 1978), are considered closer to the prehistoric Polynesian breed. For reasons already discussed, Polynesian-type pigs can be expected to possess more ancestral-type features. It is obvious that present day mountain pigs do not represent genetically pure progenies of the aboriginal Polynesian pig. "Forest pigs" generally live at lower elevations, are larger than "mountain pigs," do not have high shoulders, possess all types of coat colors and are derived from more recent breeds. Perhaps the epithets "early type" and "recent type" are more appropriate descriptives for the "mountain pig" and the "forest pig."

(iii) Feral pig eradication program, 1910-1958.—Governmental efforts to control feral pigs on all major islands began in the early 1900s when the Hawaii Territorial Board of Agriculture and Forestry observed that the destruction of native forests by pigs was unacceptable for the preservation of watershed and native forestry. Pigs removed the forest understory, were responsible for the loss of native plants and progressive deterioration of the native forests. The Board formed a Noxious Animal Eradication Program. From 1910-1958, a "ruthless eradication campaign" was mounted against the pigs. The campaign, described as "incessant warfare" was intensive, being interrupted only by World Wars I and II. The principal control technique was shooting. Members of the Civilian Conservation Corps were also employed to assist in shooting the pigs. In more remote areas shooting was supplemented with dog-hunting, which proved effective. Poisons were used experimentally but were found to be ineffective; the identity of the poison(s) was not recorded in any of the reports examined.

A total of 169,592 pigs were shot from all the islands during the 48-year period (Table 5). The island of Hawaii yielded the largest harvest for each biennium, with Oahu, Kauai, Maui and Molokai following. Kill statistics show an increasing harvest over the years,

TABLE 5 : Kill statistics for feral pigs shot on all Hawaiian islands in the Eradication of Destructive Wild Stock Program administered by the Hawaii (Territory) Board of Agriculture and Forestry, 1910-1958.

Period	Number of pigs killed					Total
	Kauai	Oahu	Molokai	Maui	Hawaii	
1917-1918			--all islands--			397
1919-1920			--all islands--			435
1921-1922			--all islands--			471
1923-1924			--all islands--			494
1925-1926			--all islands--			1,921
1927-1928			--all islands--			2,609
1929-1930	289	938	29	543	4,811	6,610
1931-1932*	1,544	3,834	188	226	5,601	11,393
1933-1934	1,100	1,961	150	45	3,744	6,901
1935-1936	1,163	2,321	67	243	3,921	7,721
1937-1938	1,294	1,337	21	100	5,483	8,235
1939-1940	1,377	1,503	12	152	6,823	9,868
1941-1942	516	504	4	222	5,031	6,277
1943-1944	195	556	24	263	1,513	2,558
1945-1946	509	891	28	363	2,471	4,262
1947-1948	2,093	2,361	118	1,291	13,841	19,704
1949-1950	2,302	1,695	73	2,456	15,989	22,515
1951-1952	1,213	1,384	20	1,300	14,378	18,295
1953-1954	1,269	1,514	35	1,006	13,077	16,901
1955-1956	1,054	1,611	130	793	13,639	15,318
1957-1958	671	1,760	139	597	14,933	18,100
1917-1958	8,602	10,325	515	7,443	85,857	169,592

* Statistics extracted from Hawaiian Forester and Agriculturalist (1933), Vol. 30(1). Data for all other years are extracted from Hawaii (Territory) Board of Commissioners of Agriculture and Forestry reports.

despite essentially continuous eradication (shooting) efforts. This may be suggestive of an underexploited population, low initial hunting effort or increased fecundity at lower densities. Control by shooting was obviously a function of shooting effort. The depression in 1931 caused many men to turn to pig hunting; the Oahu kill was four times higher than the previous biennium and the all-island total was 17 times higher than the previous biennium (Table 5). The shooting program greatly reduced the number of pigs on the islands of Kauai, Oahu and Hawaii. On Oahu alone, feral pigs were thought to have been nearly exterminated by the shooting (Tinker 1938). Control efforts by shooting include recreational hunting, sport hunting and deputized shooting has continued to the present day. Kill statistics from 1960-1970 averaged 20,000 pigs annually statewide; with an estimated population of 80,000. Since 1970, annual total kill for all the islands ranged from 7,500 to 11,000. The decline in harvest has been attributed to predation by feral dogs and overhunting in some areas.

(iv) Impact on native ecosystem.—Relatively little is known about the dynamics and long term effects of pig-produced perturbations on natural insular ecosystems. Giffin's (1978) study is the only previous major research on an insular population of pigs, but his study was designed to provide data for effective management of the pig as a game mammal. Despite our limited knowledge of pig-habitat interactions, several negative impacts resulting from pig activities have been established. These and other postulated impacts may be summarized as follows: decline of the native goose, Branta sandivencis (and other ground-nesting species), through egg and gosling predation (Bryan 1937; Baker 1979; Kear & Berger 1980; Warshauer 1980); destruction of ground cover and forest understory leading to erosion (Tillett 1937; Warner 1959); loss of native plant species through direct feeding (Beccari & Rock 1921; Lamb 1938; Baker 1975, 1979; Degener & Degener 1977; Giffin 1977, 1978); actively dispersing exotic plant species by endozoochory (Warshauer 1980); change in plant species composition favouring nonnative species (Lamb 1938; Spatz & Mueller-Dombois 1975; Jacobi 1980; Yoshinaga 1980); impacting native stream biota by increasing soil sediment load (Kinzie & Ford 1977); spreading of root-rot fungi and loss of native trees (Laemmlen & Bega 1972; Baker 1979); facilitating the breeding and spread of disease-carrying mosquitos through its wallows and hapu-feeding habits (Baker 1979); damage to pasture lands (Giffin 1978); and damage to agricultural crops such as sugar-cane and macadamia nuts (Giffin 1978).

(v) Feralization: A hypothesis explained.--When were pigs feralized? The possibility exists that the time of feralization can be estimated from the extent of damage to forest ecosystems. It is generally believed that native forest deterioration resulting from pig activities is relatively recent. Arguments for the contention that native forest deterioration occurred during the post-European era, rather than in Polynesian times have been centered on the following hypotheses:

Hypothesis 1: The Polynesian pig was not prone to ferality and may not have become feral. This opinion has been expressed by Cooray, in Mueller-Dombois et al. 1981 who also quoted Lamoureux's observation that pigs on some Pacific islands do not appear to become feral.

Hypothesis 2: If the Polynesian pig did become feral, its impact on native forest was insignificant owing to its relatively smaller size. This opinion has been formally expressed by Warshauer (1980) and several contemporary naturalists.

Both hypotheses are examined to determine if they support the view that deterioration of forests has occurred in post-European times. Hypothesis number two assumes body size to be a determinant of damage. Rooting is a food-searching behavior found in all pigs, among which <u>Sus</u> are true rooters. The relatively smaller size of the Polynesian pig is an early-type character. Body size cannot be used to imply that it is less of a rooter. Rather than size, animal density and the extent of feralization would be more important population characteristics determining habitat damage. Hypothesis number two is considered untenable under the present evaluation.

Hypothesis number one assumes breed uniqueness and a strong domesticator-domesticant, that is, Polynesian (man-pig) relationship. Pigs, including the Polynesian breed, are very prone to feralization. Given inducements and opportunities, domestic pigs easily revert to a feral state of existence (Tringham 1969). Grzimek (1972) noted that there is hardly another domestic animal more inclined to return to the wild state than the pig. As early as 1777, Cook while releasing a boar and a sow on Van Diemen's Land wrote that "as that race of animal soon becomes wild and is fond of the thicket cover of the woods, there is great probability of their becoming preserved..." (Cook 1784, Vol. I p. 98). Having at different times left in New Zealand "not less than ten or a dozen hogs, besides those put on shore by Captain Furneaux," Cook wrote that "it will be a little extraordinary if this race should not increase and be preserved here, either in a wild or in a domestic state or in both" (Cook 1784, Vol. I p. 132). Cook's remarks for the species was true for the Polynesian pig, which had run wild on many islands (British Admirality 1945, Vol. I p. 182). Reversion from domesticity to the feral state of pigs transported from island to island accounted for their presence on most of the settled Polynesian islands. The assumption of a strong Polynesian (man-pig) association in Hypothesis number one is not valid either. In prehistoric times, pig rearing was characterized by a very loose domesticator-domesticant bond. This observation will be discussed in greater detail below. Under this type of management, it is inevitable for animals to detach themselves from a herd, and from man to begin existence in the wild state.

Having considered both hypotheses as untenable, and proposed that the Polynesian pig was prone to feralization, it follows that feral populations should have been well-established, undergone population eruptions (Caughley 1970), and impacted native forest in precontact times. But this does not appear to be the case. Forest deterioration, which must have begun in Polynesian times, was minor but became significant and was accelerated only after European contact (British Admiralty 1945, Vol. I p. 169). This suggests that:

[1] although the pig could revert to feral existence, the feral state of existence was not extensive and not the predominant state of existence in precontact times;

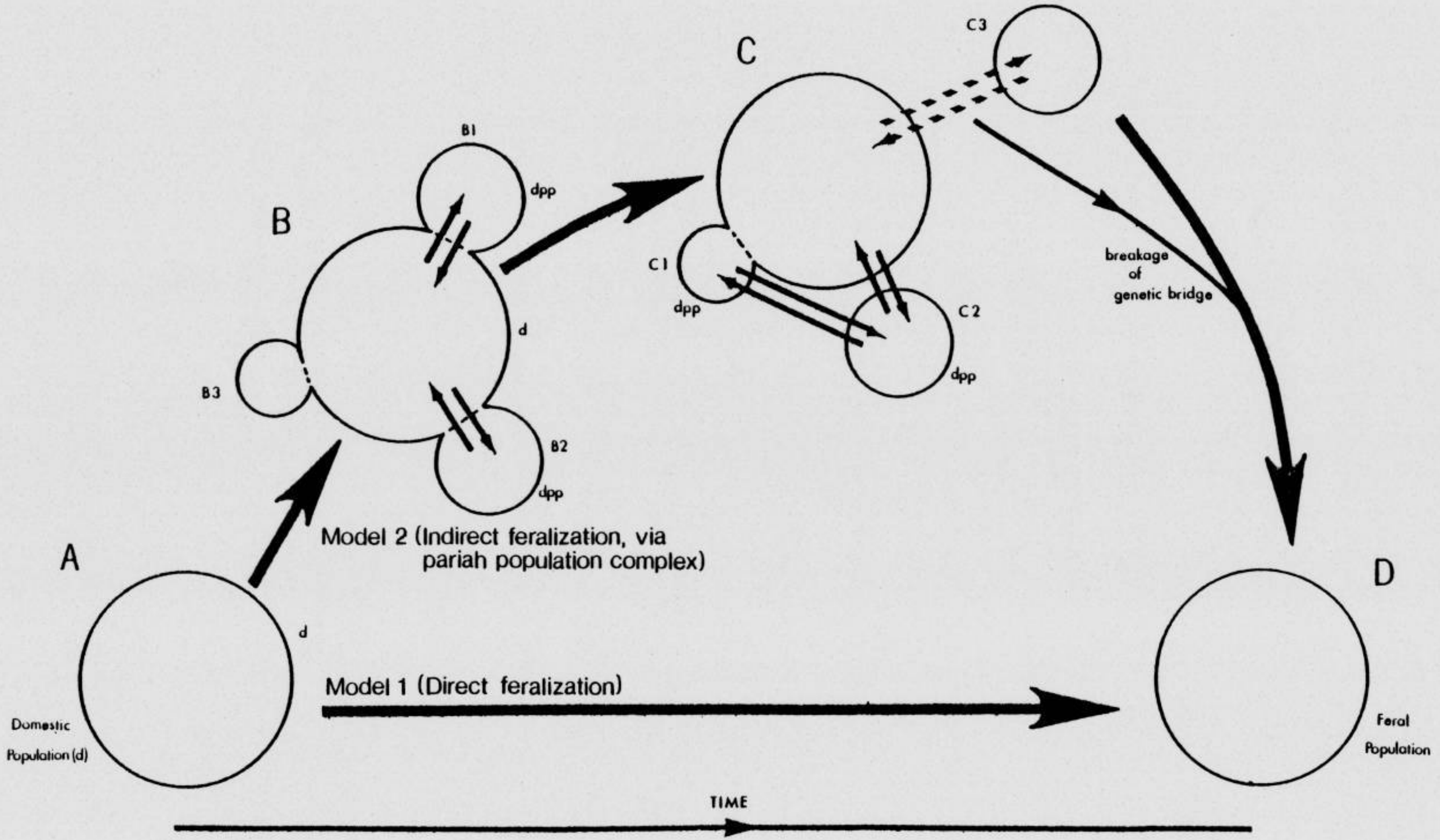
[2] in precontact times some process must have been in operation to delay feralization.

Unlike Caughley (1970), who considers postliberation eruption as a local rapid rise to high numbers, Elton (1958) noted that there is a long period that often elapses between first introduction of species and its rise to large numbers. But the latter did not offer any reason for his observation.

This dissertation proposes the "pariah population complex" hypothesis as an alternative hypothesis to explain the apparent delayed feralization and hence lesser degree of native forest destruction in Polynesian times. This alternative hypothesis is that pigs in precontact era in Hawaii, Polynesia and elsewhere in Oceania, existed for the most part as pariah and pariah-domestic populations. These predominant states of existence impeded the feralization process, which was accelerated by a multitude of factors in the post-European era.

The "pariah population complex" hypothesis is developed by examining Bokonyi's (1969) three components of the domestication process. The only relevant interactive arm in Oceania is that of domesticator-domesticant, that is, Polynesian (man-pig) interaction. When the domesticator-domesticant interaction is strong, as when man exercises direct control over his animals, a rigidly managed domestic population may be described (Figure 3). Under this domestic management, animal breeding is directly controlled by man; its sustenance and shelter are also provided by man. This management practice requires containment of animals by enclosures or fencing. Domestic pig management of this type did not exist in the Hawaiian islands, elsewhere in Polynesia or in Oceania. In the pre-European contact era, Polynesian man-pig interaction was essentially a loose one, consisting of the pariah, and pariah-domestic states of existence, which this dissertation contends are the predominant and most important states of existence for the pig in Polynesian times. The loose man-pig interactive bond was responsible for the development of these states of existence. Pigs were never contained by any method. They were "never confined in sites, but range about in search of food" (Ellis 1831, Vol. I p. 71). The pigs herded with dogs (Cook 1784, Vol. III p. 118), acted as scavengers, and were left unattended to roam freely and without restraint. These Polynesian pig-keeping habits must have provided inducements and opportunities for pigs to dissociate themselves from man and the general herd. The "budding effect" and drifting away of pigs, referred to as a pariah population, from the general domestic population is illustrated in Figure 3. Food is probably one of the more important factors causing animals to associate themselves less with man. Oliver (1973) observed that when the daily ration for a full grown pig falls below 2.5kg, pigs

Figure 3: Pariah population model explaining the apparent delayed feralization of pigs in Polynesian times. Note that the interaction between Polynesian man and his pig in $(B,C) < A$, negligible in C3, and none in D. Notation d denotes domestic population and dpp, denotes domestic-pariah populations. B1,2,3 and C1,2,3 respectively represent the early and later stages of domestic-pariah populations. Large arrows represent changes in population state through either time (A-B), (B-C), or due to reduced and eventually interrupted gene flow (C-D).


C3
C
B1
dpp
B
C1
dpp
C2
dpp
breakage
of
genetic bridge
d
B3
B2
dpp
Model 2 (Indirect feralization, via
pariah population complex)
A
D
d
Model 1 (Direct feralization)
Domestic
Population (d)
Feral
Population
TIME

will begin to leave man and the domestic herd. In pariah populations, the man-pariah pig interaction was considerably less than the Polynesian man-pig interaction. Sustenance and breeding are less under the control of man. Pariah pigs may be said to have the best of both worlds; they may derive occasional benefits in terms of food and shelter provided by man but are able to utilize available resources outside the general confines of the domestic population. This state of existence can contract or expand depending on food inducement and on any modifications in the strength of the Polynesian (man-pig) interactions. The domestic-pariah and pariah states of existence can continue indefinitely, and therefore impede the progression to establishment of a true feral population.

There are indications that feral populations may have existed in precontact times. Cook (1784) mentioned that pigs "were sometimes found wild in the mountains." Ellis (1831 Vol. 4 p. 24) wrote, "the hogs...were sometimes found in the mountains..." If true feral populations already existed in precontact times, it seems certain that feral populations would have interacted with pariah populations to suppress the further expansion and establishment of feral populations. In this context, pariah populations may be considered as a bridge between domestic and feral states of existence. The ecological implications behind the "pariah population complex" hypothesis are the suppression or increased resistance to the feralization process and the delay to population increase and eruption. It follows, therefore, that native forest deterioration by pigs was probably insignificant in Polynesian times.

True feral populations form when pariah populations drift further away from the general domestic population (Figure 3). Pariah pig-man and pariah-domestic pig interactions become less significant and decay with time, although occasional pariah-domestic pig interactions may still occur. When these interactive bridges are broken, a true feral population is obtained.

Events in the postcontact era contributed to and accelerated the feralization process. These included forest clearing, introduction of agriculture, ranching, and uphill recession of the forest line. Open ranch farming on the principle of "maximum pork with minimum cost" (Hollingsworth 1853) and the importation and release of pigs by upland ranchers further accelerated the establishment of feral populations. Thus, it can be seen that while pariah states of existence during Polynesian times may have delayed the feralization process it was accelerated by certain postcontact events. Native forest deterioration is therefore, in my view, a postcontact rather than a precontact phenomenon.

CHAPTER 3

KIPAHULU VALLEY RAIN FOREST ECOSYSTEM

Kipahulu Valley represents an outstanding remnant of an essentially pristine ecosystem, internationally recognized for its uniqueness, rich native biota, and high endemism. Evaluated in 1967 by a 14-member Scientific Expedition as an area whose preservation as an ecological reserve will be an asset to science, the Valley was deeded by The Nature Conservancy and the State of Hawaii to Haleakala National Park for preservation of the area in its natural state and management of its biological resources. Visited and botanized only somewhat cursorily in some instances, by Forbes in 1919 (Lamoureux 1967); Hjort and Fagerlund (1945); St. John and Mitchell in 1945; the 1967 Scientific Expedition (Warner 1967); Becking (1970); and Lamoureux and Stemmermann (1976), the Valley is a prime habitat for many rare and endangered plants and animal species, some previously thought to be extinct. The Valley is a difficult area for scientific investigation because it has a rough terrain, dense vegetation and a wet climate. This chapter describes the rain forest and forms the background against which all population processes of the feral pig are studied and described.

Topography

Haleakala National Park is comprised of two geographically separate areas--Haleakala and Kipahulu districts (Figure 4). The topography of the Valley in relation to the surrounding areas is shown in Figure 5. Within Kipahulu district, the following field regions have been

Figure 4: Map of Kipahulu Valley showing its location in Haleakala National Park and in the Hawaiian archipelago, as well as field installations and important landmark reference points. —— major trail system; K- Koukouai trail; E- central escarpment trail; L- lower plateau trail; • radiotracking stations; GS 1,2,3- germination sites 1,2,3; B,C,D- temporary shelters Bravo, Charlie, Delta; • tree blinds for observing feral pigs; DL- Dogleg. Contour lines are in feet. Alphanumerals (e.g. E700) in text refer to locations on a particular trail system and elevation, in meters, above sea level.

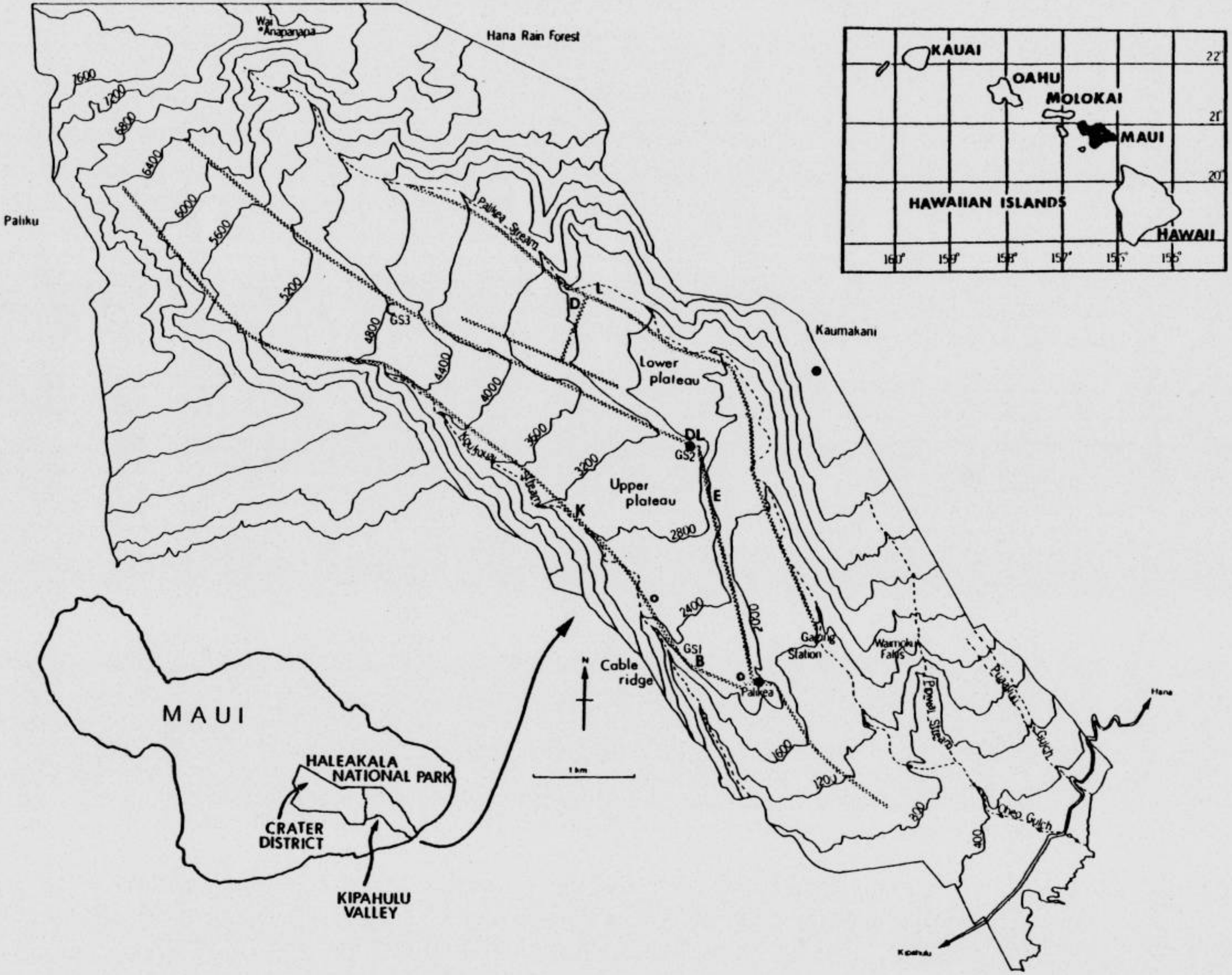
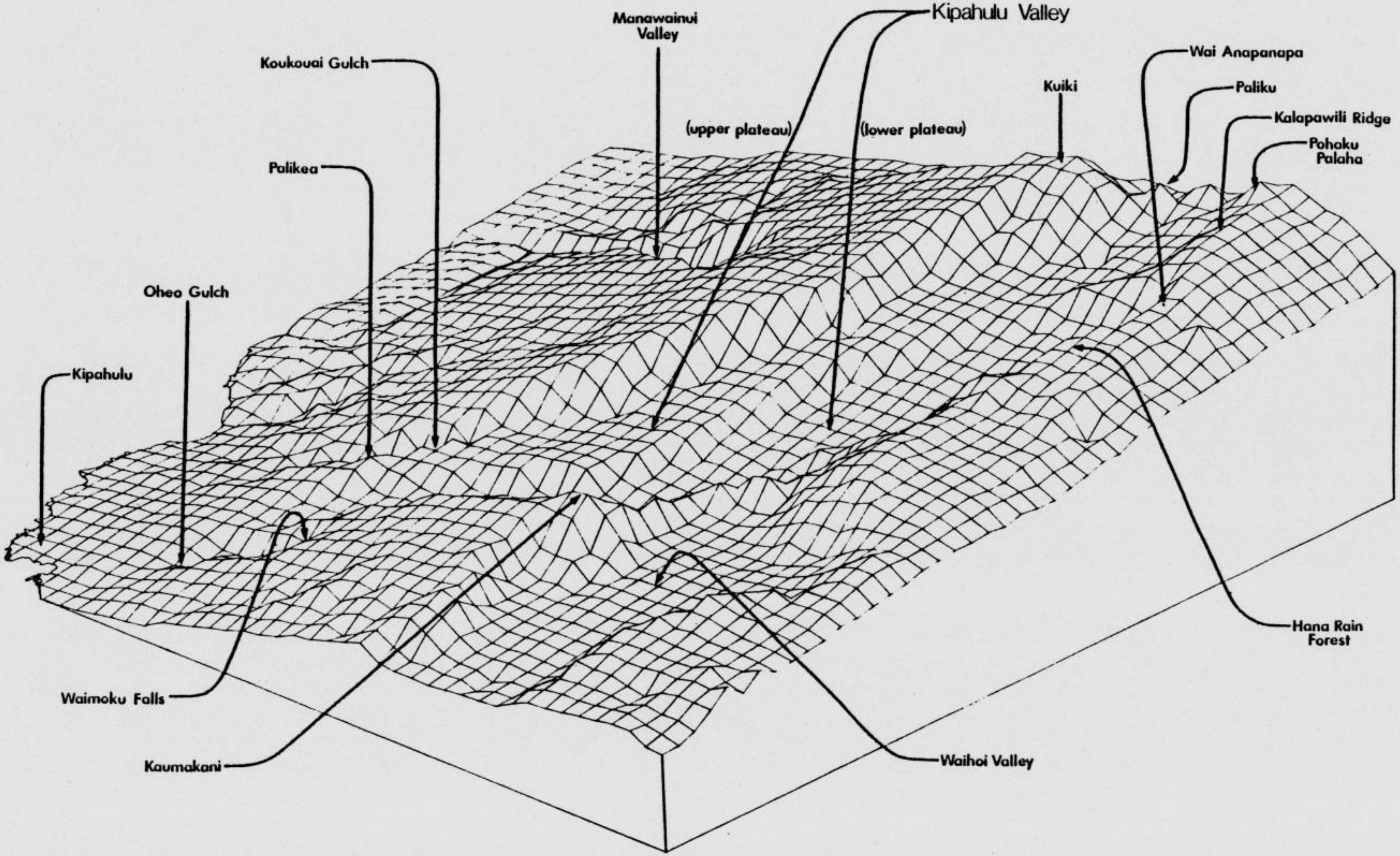

Wai Anapanapa
Hana Rain Forest
Paliku
Palikea Stream
Kaumakani
Lower plateau
Upper plateau
Kaukaua Stream
L
D
DL
GS2
GS3
E
K
B
GS1
Cable ridge
Gaging Station
Waimoku Falls
Palikea
Popolo Stream
Pipiwai Gulch
Oheo Gulch
Hana
Kipahulu
N
1 km
7600
7200
6800
6400
6000
5600
5200
4800
4400
4000
3600
3200
2800
2400
2000
1600
1200
800
400
KAUAI
OAHU
MOLOKAI
MAUI
HAWAII
HAWAIIAN ISLANDS
22°
21°
20°
160°
159°
158°
157°
156°
155°
MAUI
HALEAKALA NATIONAL PARK
CRATER DISTRICT
KIPAHULU VALLEY

Figure 5: A profile diagram of Kipahulu Valley and its surrounding areas. Note that the Valley is a topographical enclave and is bounded on both its long sides by nearly vertical walls.


Manawainui Valley
Kipahulu Valley
Koukouai Gulch
(upper plateau)
(lower plateau)
Kuiki
Wai Anapanapa
Paliku
Kalapawili Ridge
Pohaku Palaha
Palikea
Oheo Gulch
Kipahulu
Hana Rain Forest
Waimoku Falls
Kaumakani
Waihoi Valley

recognized: pastoral-agricultural region below 490m; Kaumakani Rain Forest; head of Valley above 1830m; Kuiki; southwestern plateau between 490 and 1830m; and northeastern plateau between 490 and 1830m (Smith 1978). It is on these two plateaus in the Valley proper that the present study was conducted.

The Valley runs inland in a northwesterly direction from its mouth at about 300m above Oheo to its headwalls at about 2280m at Pohaku Pahala (Fig. 5). The valley floor has two levels, separated by a sharp discontinuity generally referred to as the central escarpment or pali. The northeastern level (lower floor) is about 180m lower than the southwestern level (upper floor). Both long sides of the Valley are bordered by nearly vertical sidewalls--Kaumakani Ridge in the east and Kuiki Ridge in the west. These ridges form a topographical enclave, thus further isolating the Valley from surrounding regions.

Two deeply undercut perennial streams, both originating in the Valley, drain the area. Koukouai Stream, an intermittent stream, drains the upper plateau of the Valley and continues into Koukouai gulch. Palikea Stream, an interrupted second order stream, is the major drainage, and together with Pipiwai Stream, drains a total of 22 square kilometers (Kinzie & Ford 1977). In addition to these drainages, many gulches and streams dissect the valley at all levels. The lower reaches of Palikea, Pipiwai and Pua'alu'u Streams support an extremely delicate and potentially unstable freshwater ecosystem, consisting of the "endangered" goby _Lentipes concolor_, two other gobiids _Awaous stamineus_ and Sicydium stimpsoni and the endemic shrimp, Atya bisulcata (Kinzie & Ford 1977).

Geology

Kipahulu Valley, along with Kaupo, Keanae and Waihoi valleys were cut from the sides of Haleakala by stream erosion in prehistoric times. This event occurred during the period of volcanic quiescence after the Kula series of eruptions (Stearns & McDonald 1942). At this time the Valley was deeper and extended to the ocean. During early and late Hana times, volcanic activity subjected the Valley to two series of valley fillings, with a time interval long enough to allow weathering and erosion of lava before burial by the next flow. Early Hana flows filled the valley to a depth of more than 300 meters. Stream erosion subsequently cut a new valley (lower plateau) along the northern boundary of the early Hana valley fillings. Late Hana flows filled the stream-cut canyon and overlayed the entire earlier Kula valley to the coast. Thus, the Valley's plateaus differ in geological age and soil forming parent materials, with the eastern plateau being geologically younger.

Soils

Soils in the Valley are diverse. Four principal types can be identified: Maka'alae silty clay below 490m; Hydrandepts-Tropaquods association in the Valley proper, Hana Rain Forest and Kuiki; rough, mountainous land in Kaumakani Ridge, Wainapanapa, Valley head, central escarpment and slopes of Kuiki; and cinderland, on the upper slopes of Kuiki (Smith 1978).

Hydrandepts-Tropoaquods, Maka'ale series (Order Inceptisols) form the major soil complex in the valley floor. These are young soils developed from volcanic ash, cinder and igneous rock, high in organic content (40-60%) and amorphous materials that irreversibly dehydrate into sand and gravel-sized aggregrates (McCall 1973). This soil association when zoned is distinguished by a blackish to dark brown A-horizon averaging 8-20cm and an impermeable yellowish-red B-horizon. Hydrandepts-Tropaquods associations are found in well-drained areas, but occur generally on poorly drained soils and in bogs. Many low-lying areas have year-round standing water on this clayey impermeable B-horizon, thus creating marshes which are found at all elevations. This soil type that typifies the Valley's rain forest supports dense vegetation of Acacia koa and Metrosideros collina.

The Valley's rain forest soils are very acidic and low in detectable bases. These properties are borne out from results of an analysis of 31 soil samples collected from throughout the Valley (Fig. 6, 7). Soil pH varies from 3.3-7.1, with over 50% of the samples having a pH below 5. Calcium, phosphorus, potassium and magnesium occur in very low concentrations as extractable nutrients, indicating that the soils are highly leached.

Soil depths vary, but are generally shallow. Between 900 and 1350m elevation on the northeastern plateau, the soil is stony and there

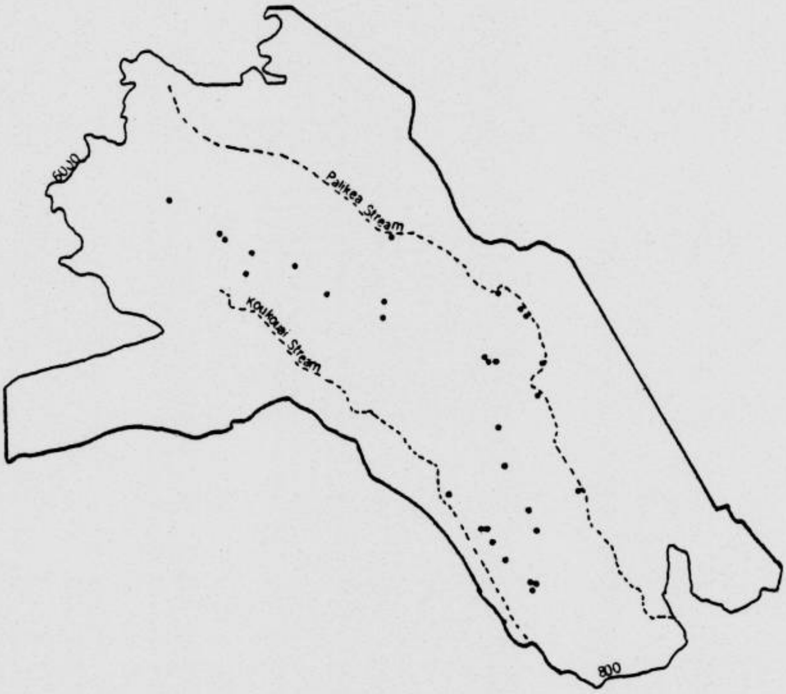


Figure 6 . Soil sampling sites in Kipahulu Valley, Maui, Hawaii.

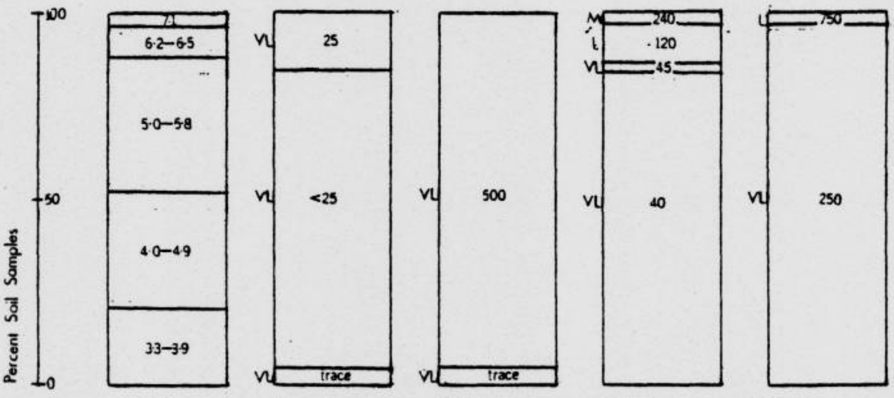


Figure 7 . Soil sample analyses results. Data are given in available extractible nutrients in pounds per acre. VL, M or L denotes very low, moderate or low nutrient availability status according to agricultural standards. Data shown here is a summarization of results of 31 soil samples analysed by the Soil Testing Service, Cooperative Extension Service, University University of Hawaii and U.S.D.A. in cooperation.

appears to be little soil formation on the pahoehoe bedrock. Most of the soil materials may have been transported. Transport of soil sediments resulting either from pig-rooting activities or natural events appears to be insignificant and localized. Fallen trees, and especially drainage pattern and topographic features encourage sediment ponding; these marshy ponds occur throughout the valley, remain wet all the year round, and are quite extensive on the lower plateau. Natural catastrophic events occurring before World War II and in the recent past are thought to account for such observations as charcoal in subsoil, deep gully erosion and top soil sheet erosion believed not to be produced by pigs (Eckern 1979 - pers. comm.).

Climate

Climatological data for Kipahulu Valley are nonexistent, primarily because of its inaccessibilty. Northeasterly trade winds strike the Valley almost perpendicularly. Averaging about 30km/hour, these winds are generally funnelled up the Valley and into the Crater above Paliku. Unusually strong winds in excess of 120km/hour were encountered during this study. No dry season was observed during the period of this study. Heavier precipitation occurs during winter with storms from October to April. However, long periods of heavy rain during the remaining months and even during summer, are not uncommon. The minimal annual rainfall has been estimated at about 3080mm (Blumenstock & Price 1967), but maximal precipitation could be in excess of 7620mm. Nothing is known about fog drip which is extensive and may contribute significantly to the annual precipitation.

The National Oceanic and Atmospheric Administration (N.O.A.A.) maintains two weather stations in the Park. Haleakala RS 338 (2142m) records precipitation and temperature, while Kipahulu 258 (79m) records precipitation only. Mean monthly temperatures and mean monthly precipitation for Haleakala and Kipahulu, summarized from N.O.A.A. 1979 Vol. 13 and N.O.A.A. 1980 Vol. 76 No. 1-12 are diagrammatically shown in Figure 8. Mean monthly relative humidity and mean monthly temperature for Kipahulu Valley recording stations B (655m) and C (1477m) are shown in Figure 9. Mean monthly relative humidity at stations C and B averages 92.9% and 87.27%, with mean monthly relative humidity varying between 86.56-96.9% and 82.6-91.9% respectively. Mean annual temperatures at stations B and C are 19.8°C and 15.0°C, with temperatures ranging from 13.7-25.5°C and 8.1-21.1°C respectively, and a mean temperature difference between the stations of 4.8°C over an altitude difference of 792m. This temperature difference between the stations is slightly larger than the expected calculated difference (hence lower mean annual temperature at station C) when the calculation is made referencing station B and using the adiabatic lapse rate of 3°F/1000ft. This difference is because the Valley above 3000ft. is in the cloud inversion zone. In general, temperature range increases with altitude; the average temperature at station B is 11.8°C, at station C is 12.9°C and at Haleakala RS 338 (for 1979) is 24.4°C. Temperature variations and their extreme values may be biologically more important than the mean value for the adaptation of some rain forest organisms.

Figure 8: Mean monthly temperature and precipitation for weather stations Haleakala RS 338 (2142m) and Kipahulu 258 (79m). Bars represent precipitation and open circles represent temperature. Kipahulu 258 records precipitation only. Diagrams are constructed using the 1979 and 1980 data from the National Oceanic and Atmospheric Administration (NOAA) Annual Summary, Volume 75, Number 13 and from NOAA Volume 76, Numbers 1-12 respectively.

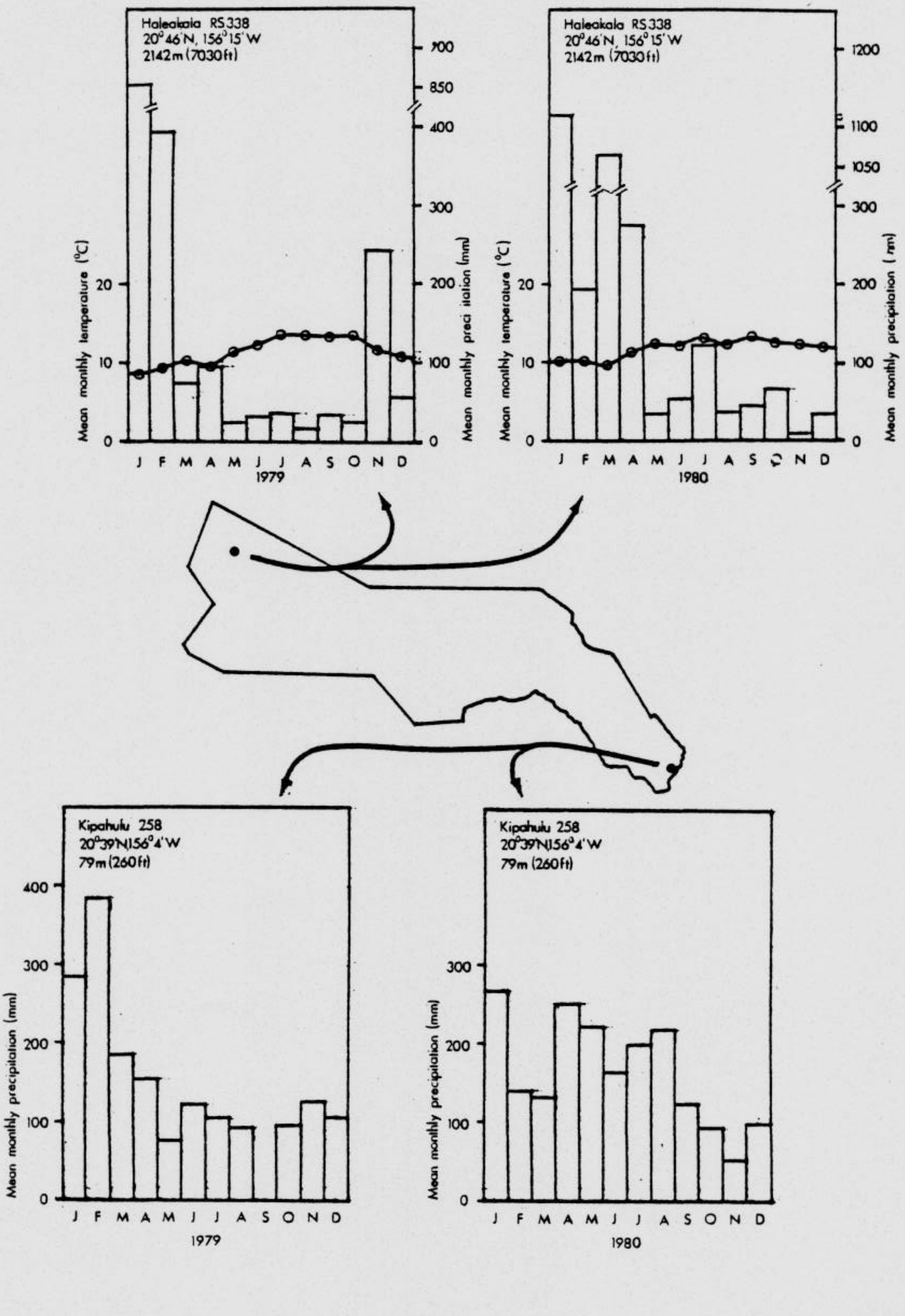
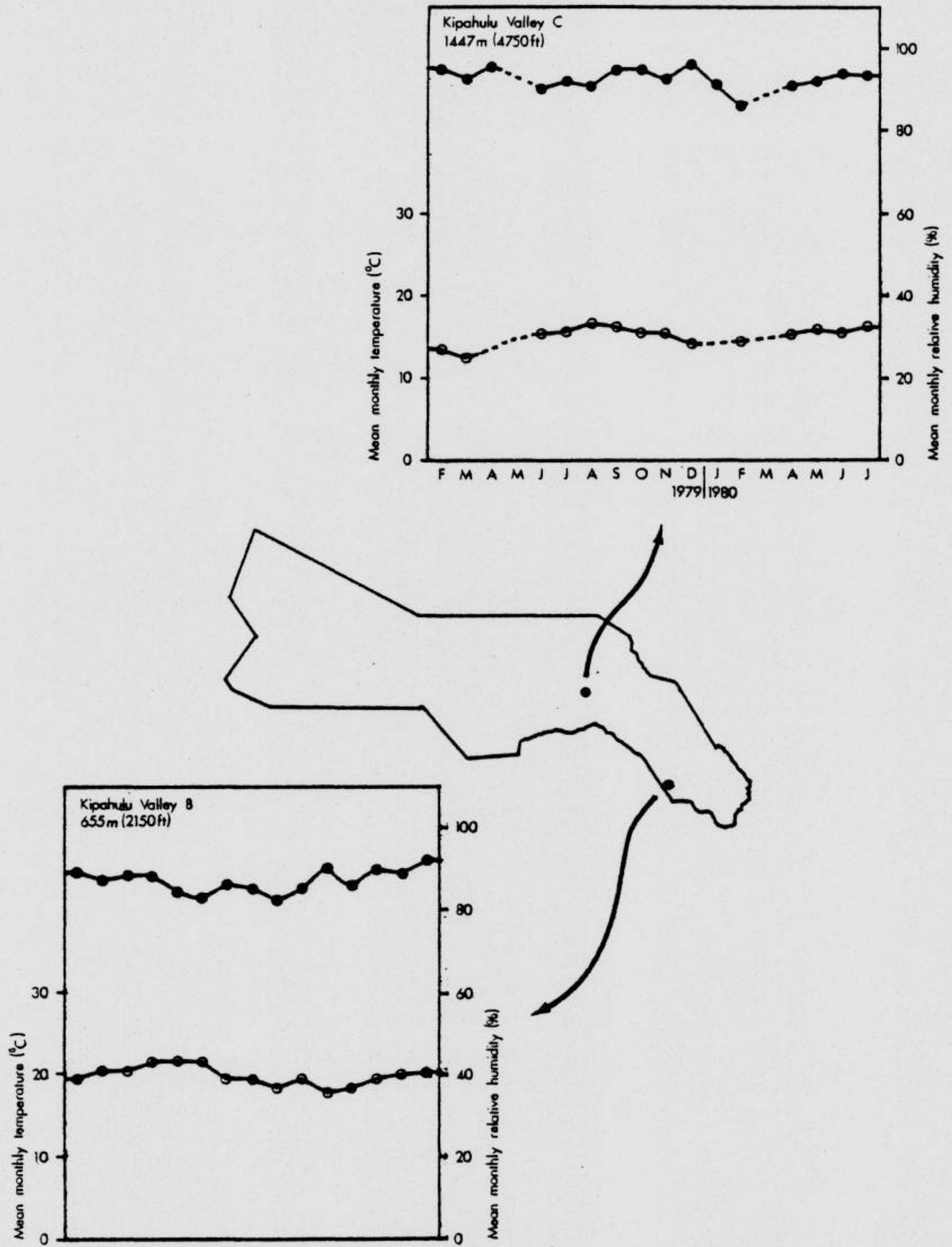

Haleakala RS338
20°46'N, 156°15'W
2142m (7030ft)
Mean monthly temperature (°C)
Mean monthly preci itation (mm)
0
10
20
0
100
200
300
400
850
900
J F M A M J J A S O N D
1979
Haleakala RS338
20°46'N, 156°15'W
2142m (7030ft)
Mean monthly temperature (°C)
Mean monthly precipitation (nm)
0
10
20
0
100
200
300
1050
1100
1200
J F M A M J J A S O N D
1980
Kipahulu 258
20°39'N,156°4'W
79m (260ft)
Mean monthly precipitation (mm)
0
100
200
300
400
J F M A M J J A S O N D
1979
Kipahulu 258
20°39'N,156°4'W
79m (260ft)
Mean monthly precipitation (mm)
0
100
200
300
J F M A M J J A S O N D
1980

Figure 9: Mean monthly temperature and relative humidity for Kipahulu Valley stations B (K655m) and C (E1447m). Temperature and humidity were recorded with a recording hygrothermograph. ● - mean monthly relative humidity; o - mean monthly temperature.


Kipahulu Valley C
1447 m (4750 ft)
Mean monthly temperature (°C)
0
10
20
30
Mean monthly relative humidity (%)
0
20
40
60
80
100
F M A M J J A S O N D J F M A M J J
1979 1980
Kipahulu Valley B
655 m (2150 ft)
Mean monthly temperature (°C)
0
10
20
30
Mean monthly relative humidity (%)
0
20
40
60
80
100
M J J A S O N D J F M A M J J
1979 1980

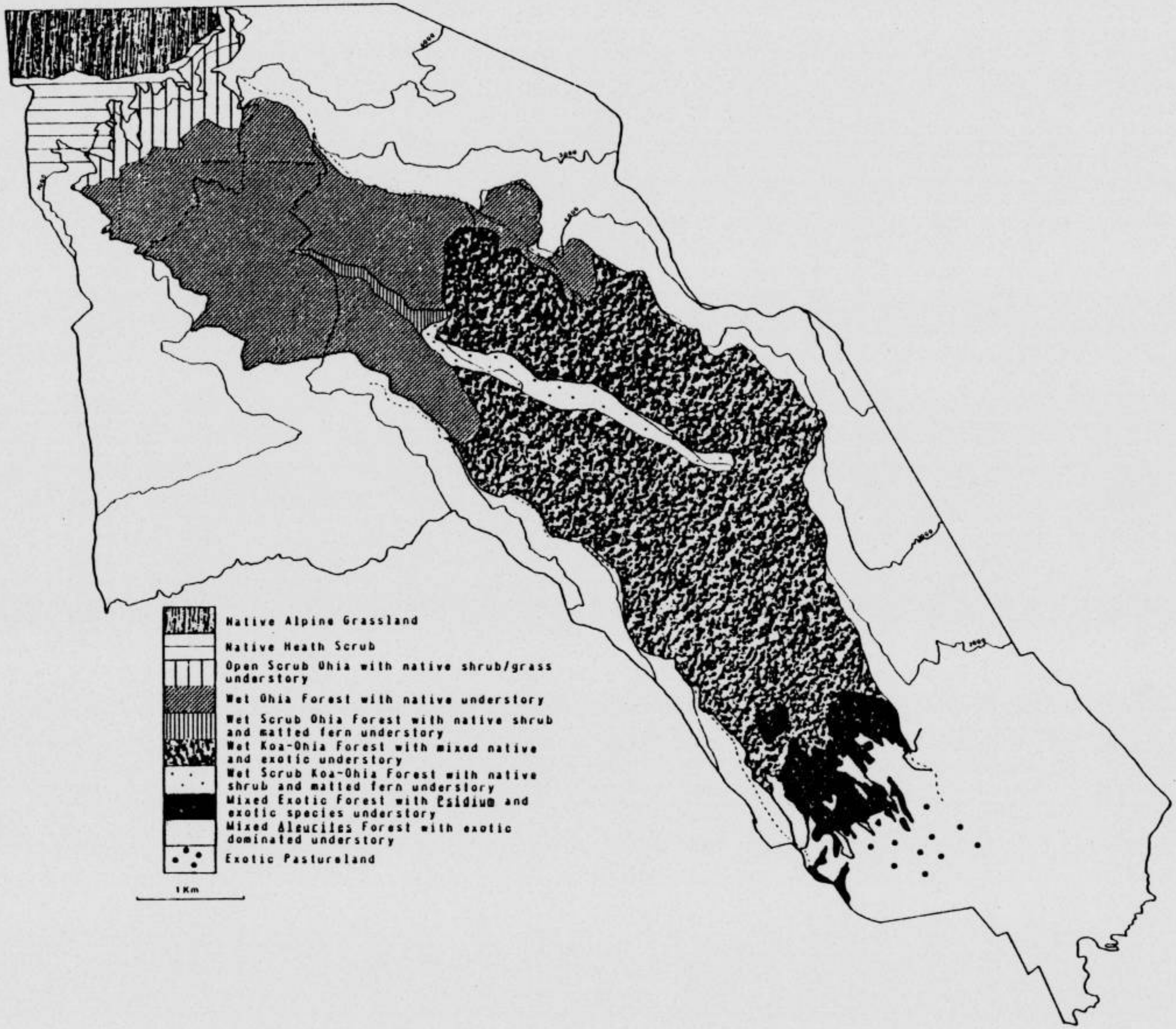
Terrestrial Ecosystem

(a) Plant communities

Plant communities in the Valley have been described as diverse, complex, and offering unparallelled research opportunities. Within a five kilometer distance are communities ranging from tropical rain forest to a subalpine zone. Smathers (1967) identified and mapped 19 vegetation types using the 1965 U.S.G.S. aerial photographs. Using field surveys, aerial photographs and 1977 U.S.G.S. orthophotoquad maps as base, Jacobi (1981 unpubl. data) recently mapped ten generalized vegetation types for the entire Valley (Fig. 10). Analysis of aerial photographs over the last 15 years has not demonstrated any structural changes in the forest canopy, although canopy and ground cover changes in the Palikea area have changed remarkably over this period in association with the spread of strawberry guava (Smith 1978).

Plant communities are described here with reference to Figure 10, Smathers (1967), Yoshinaga (1980) and from field observations. The coastal lowland ecosystem, from 460m to sea level is comprised of grasslands, woodland, streams, ocean-spray zone and the coastal waters (Smith 1981). Patches of Psidium guajava, P. cattleianum, Mangifera indica, and Aleurites moluccana are interspersed in the gulches and exotic grassland—once an agricultural area. The last mentioned species is believed to be a relict of the lowland forest stabilized after Polynesian colonization. From 460 to 610m a mixed two-storied forest becomes evident, with the dominant species Acacia koa, Aleurites

Figure 10: A generalized vegetation map for Kipahulu Valley, Haleakala National Park, Maui, Hawaii. Map shows ten general vegetation types and was compiled at 1:24,000 scale, using the 1977 United States Geological Survey orthophotoquad maps as a base. Diagram was constructed using unpublished data provided by Jim Jacobi, U.S.Fish and Wildlife Service, Hawaii.


Native Alpine Grassland
Native Heath Scrub
Open Scrub Ohia with native shrub/grass understory
Wet Ohia Forest with native understory
Wet Scrub Ohia Forest with native shrub and matted fern understory
Wet Koa-Ohia Forest with mixed native and exotic understory
Wet Scrub Koa-Ohia Forest with native shrub and matted fern understory
Mixed Exotic Forest with Psidium and exotic species understory
Mixed Aleurites Forest with exotic dominated understory
Exotic Pastureland
1 Km

moluccana and Cheirodendron trygynum forming the upper stratum and the lower story formed by Psidium guajava, P. cattleianum, and Cibotium sp. In pure stands of Eugenia jambos forest which occur at about 610m, the stratification is lost. Here, the well-shaded forest floor is devoid of understory and ground cover. Eugenia jambos appears to be the only species able to forestall establishment of the aggressive woody weed, Psidium cattleianum, which otherwise forms dense thickets along this segment. This species is currently distributed up to 1200m. Freycinetia arborea, a woody vine epiphytic on the lower story subdominants, and also on Acacia koa, becomes common above 610m. Ground cover consists mainly of Rubus rosaefolius, Paspalum conjugatum, Athyrium sp. and other exotics. Several tree snails make their first appearance at about 550m in this mixed Acacia-Aleurites-Psidium-Eugenia forest. Up to 1070m, Acacia koa is dominant relative to cover, density, and frequency. It forms the upper story with Cheirodendron trigynum. Metrosideros collina becomes more prominant with increasing elevation, and a Metrosideros-Cheirodendron association dominates, while Acacia koa recedes with increasing elevation. In the lower story, Freycinetia arborea, Clermontia, Cheirodendron, Tetraplasandra, and Scaevola form epiphytic and sinusial relationships with Cibotium species.

A transition zone from koa to ohia forest occurs from 1000 to 1220m. At the upper limit of this zone, a Metrosideros-Cheirodendron association becomes the dominant forest cover; the lower story shrubs consisting mostly of Pelea sp., Broussaisia arguta and Scaevola chamissoiana. Ground cover is mostly ferns. Many ohia trees have prop roots. Several species such as *Cheirodendron*, *Styphelia*, *Astelia* and ferns are epiphytic on the moss-laden ohia trees. Smathers (1967) hypothesized that prop-root development and epiphytic associations may be due to adaptation to the very wet, waterlogged and highly hydric soils. From about 1370 to 2130m, the community is dominated by closed scrubby-type *Metrosideros collina* grading to a low, scattered, globose type at higher elevations. The lower story when present consists of *Cheirodendron trigynum*, *Broussaisia arguta*, *Astelia* sp. and *Styphelia*, all of which can be epiphytic.

At about 1740m, a three-layered forest appears. *Metrosideros* forms the upper story, *Cheirodendron* the second, and *Coprosoma montana*, *Styphelia* sp. and *Cibotium* the third layer. At about 1920m, a four-layered stratification is recognized with *Metrosideros* in the first stratum, *Cheirodendron* in the second, *Styphelia* sp. and *Vaccinium* in the third, and *Broussaisia* sp., *Pelea* sp. and young *Cheirodendron* in the fourth stratum. *Metrosideros* becomes widely scattered with increasing elevation and at 2220m there is an abrupt transition to *Deschampsia*, a grassland vegetation type.

Despite the drainages already described, waterlogged areas, marshes, bogs and sediment ponds occur at all elevations and these characterize the valley floor. Species composition in these openings and along steep slopes, streams and gulches are quite distinctive. *Metrosideros collina* forest is spotted with boggy openings vegetated principally by the native sedge, *Carex alligata*, and also by *Eupatorium adenophorum*. Sediment ponds and pig scarified areas are inhabited by weedy species such as *Paspalum conjugatum*, *Cyperus brevifolius* and *Erechtites* (Yoshinaga 1980). Marshes and sediment ponds between 610 and 850m along the northern edge in the lower plateau support few scattered stunted ohia and koa trees, and are dominated by *Machaerina angustifolia* and carpeted by *Hydrocotyle verticillata*. Stunted plant forms in these marshes may result from toxic end products of anaerobic processes enhanced by water-logged conditions. Riparian vegetation is characterized by species such as *Rubus rosaefolius*, *Eupatorium riparium*, *Cuphea carthagiensis*, *Youngia japonica*, ferns and *Prunella vulgaris* (Yoshinaga 1980). On steep slopes as well as along stream banks between 1100 and 1400m, isolated stands of *Gunnera mauiensis* and *Cyanea* sp. have been observed.

It is apparent that the Valley has many outstanding botanical features. Occurrence of such a wide variety of plant communities over a relatively short distance is outstanding. In an area of less than 16 square kilometers, there are 80 species of ferns, all but one of which are native; and 227 species of flowering plants, of which 66% are native species (Lamoureux 1967). There are fewer exotic species in the *Metrosideros collina* forest; and most introduced species occur in the *Acacia koa* forest below 1220 meters. In the recent past, the species pool for exotics in the koa forest and at lower elevations have increased (Yoshinaga 1980); those that have increased remarkably in species numbers are represented by the families Poaceae (grasses), Asteraceae (daises) and Cyperaceae (sedges).

(b) Vertebrate fauna

All mammals in the Valley are introduced species and of concern in resource management (Banko & Wilson 1967). These are represented by one ungulate, the feral pig, Sus scrofa; two canids, the feral dog, Canis familiaris, and the Indian mongoose, Herpestes auropunctatus; and four rodents, the roof rat, Rattus rattus, Norway rat, Rattus norvegicus, Polynesian rat, Rattus exulans and the house mouse, Mus musculus, all in the Valley interior; and by a second ungulate, the feral goat, Capra hircus, along the headwall and ridges of the Valley and beyond. The ecological interactions of these mammalian species with one another and with the avifauna, if any, are unknown.

The Valley's rain forest is a sanctuary for several species of rare and endangered birds, including the recently rediscovered endangered Maui Nukupu'u, Hemignathus lucidus affinis, Maui Parrotbill, Pseudonester xanthophrys, crested honey-creeper, Palmera dolei (Banko & Wilson 1967; Warner 1967) and other native species. Occurring in larger numbers at the middle and upper elevations up to 2130m are drepaniids, such as the apapane, Himatione sanguinea; amakihi, Loxops virens wilsoni; iiwi, Vestiaria coccinea; and Maui creeper, Loxops maculata newtoni. Other than the species inventories by the 1967 Scientific Expedition and more recently by Conant and Stemmermann (1980), nothing is known about the distribution, population size and biology of these native birds. It has, however, been hypothesized that the decline in native species might be linked with the transmission of bird pox and bird malaria by the introduced night mosquito, *Culex pipiens fatigens* (Warner 1967).

(c) Invertebrate fauna

Invertebrate life-forms, particularly entomofauna, have been described as extremely rich but poorly known. The essentially native montane rainforest provides microhabitats for many native insects. Preliminary evaluation of the entomofauna in the Valley interior has yielded over 60 species of endemic Drosophilidae and a tally of over 70% endemism in the general arthropod fauna (Warner 1967).

Oligochaetes in the Valley have not been studied. As part of the feral pig food habits study, nine species of earthworms (Chapter 6) belonging to three families were recorded from 640 to 1590m. Glossoscolecidae, a purely American family (Gates 1972), is represented by *Pontoscolex corethurus* Muller 1857. Lumbricidae, a holarctic family endemic to eastern North America, Europe and Asia, was represented by *Eisenia eiseni* Levinsen 1884 and *Aporrectodea turgida* Eisen 1872. A majority of the oligochaete fauna in the Valley are of asiatic origin and belong to Megascolecidae: *Amynthas corticus* Kinberg 1867, *A. gracilis* Kinberg 1867, *A. minimus* Horst 1893, *Lampito mauritii* Kinberg 1867, *Metaphine californica* Kinberg 1867, and *Periongx excavatus* Perrier 1872. Three species, *Eisenia eiseni* Levinsen 1884, *A. turgida* and *L. mauritii* Kinberg 1867 are new records for the Hawaiian islands. This recorded list should be considered preliminary, since any species that man has been unwittingly carrying around the world with his live plants is likely to be found in the study area.

The molluscan fauna comprises at least 18 species of land snails, distributed among three native and two exotic families (Table 6). Valley-wide, *Succinea*, *Tornatellides* and *Tornatellaria* are the more commonly represented and widely distributed forms. *Portulina porcellana* is the rarest species in the Valley, the largest native species is *Perdicella carinella* Baldwin and the smallest is a species of *Philonesia*. Distribution of the molluscan fauna appeared to be discontinuous and restricted in its abundance to narrow ranges of elevation. This discontinuity appears to be correlated with loss of, or gaps, in the continuity of herbaceous species. *P. carinella* and *Auriculella crassula* Smith are common between 550 to 670m; *Succinea* from 600 to 700m and 1160 to 1460m along the central escarpment. *Succinea*, *Tornatellides* and *Tornatellaria* are, however, more abundant and uniform in distribution on the steep north-facing, pig-free slopes of the central escarpment at 1100m. Host plant specificity is shown by the land snails; the six most important plants are *Eugenia jambos* L., *Carex alligata* F. Boot, *Eupatorium adenophorum* Spreng., *Alyxia olivaeformis* Gaud., *Broussaisia arguta* Gaud., and *Ilex anomala* H. & A.

TABLE 6 : Land snails in Kipahulu Valley, Maui, Hawaii.†

Family / Species	Host Plant / Habitat
Achatinellidae	
*Auriculella crassula**	*Eugenia jambois*, *Metrosideros polymorpha*, *Perrottetia sandwicensis*, *A. olivaeformis*
Elasmias sp.*	*Eugenia jambois*, *Eupatorium adenophorum*, *Ilex* sp.
*Partulina porcellana**	*Eugenia jambois*, *Metrosideros polymorpha*
*Perdicella carinella**	*Alyxia olivaeformis*, *Smilax*, *Metrosideros polymorpha*, *Gouldia hillebrandii*
Tornatellaria cf. *thaanumi***	*Eupatorium* sp., *Carex alligata*
*Tornatellaria cincta**	*Ilex* sp., *Carex alligata*
Tornatellides A. cf. *inornatus***	*Carex alligata*, *Ilex* sp., *Eupatorium adenophorum*, *Metrosideros polymorpha*
Tornatellides B. cf. *procerulus***	*Carex alligata*, *Eupatorium* sp., *Myrsine*, *Pelea*
*Tornatellides irregularis***	*Pelea* sp., *Carex alligata*
Euconulidae	
*Philonesia perlucens**	*Eugenia jambois*, *Ilex* sp., *Carex alligata*
Philonesia sp.*	*Eugenia jambois*, *Carex alligata*, *Eupatorium* sp.
Bradybaenidae	
*Bradybaena similaris****	*Paspalum conjugatum*, leaf litter, pig carcass
Oleacinidae	
*Euglandina rosea****	forest floor, pastureland
Succineidae	
*Succinea apicalis***	*Carex alligata*, *Broussaisia arguta*, *Eupatorium* sp., *Rubus hawaiiensis*, *Athyrium* sp,
Succinea lutulenta **	*C. alligata*, *R. hawaiiensis*, *Athyrium* sp., *Dubantia* sp., *P. cattleianum*, leaf litter
Succinea sp.**	*Carex alligata*, *Eupatorium* sp., leaf litter, *Athyrium* sp.
Zonitidae	
*Oxychilus alliarius****	leaf litter, decaying logs, bark
*Oxychilus cellarius****	*Freycinetia arborea*, forest floor, decaying logs, leaf litter

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† Checklist should be considered perfunctory as it represents species encountered while conducting observations on pig rooting and foraging habits.

* = endemic

** = native

*** = introduced

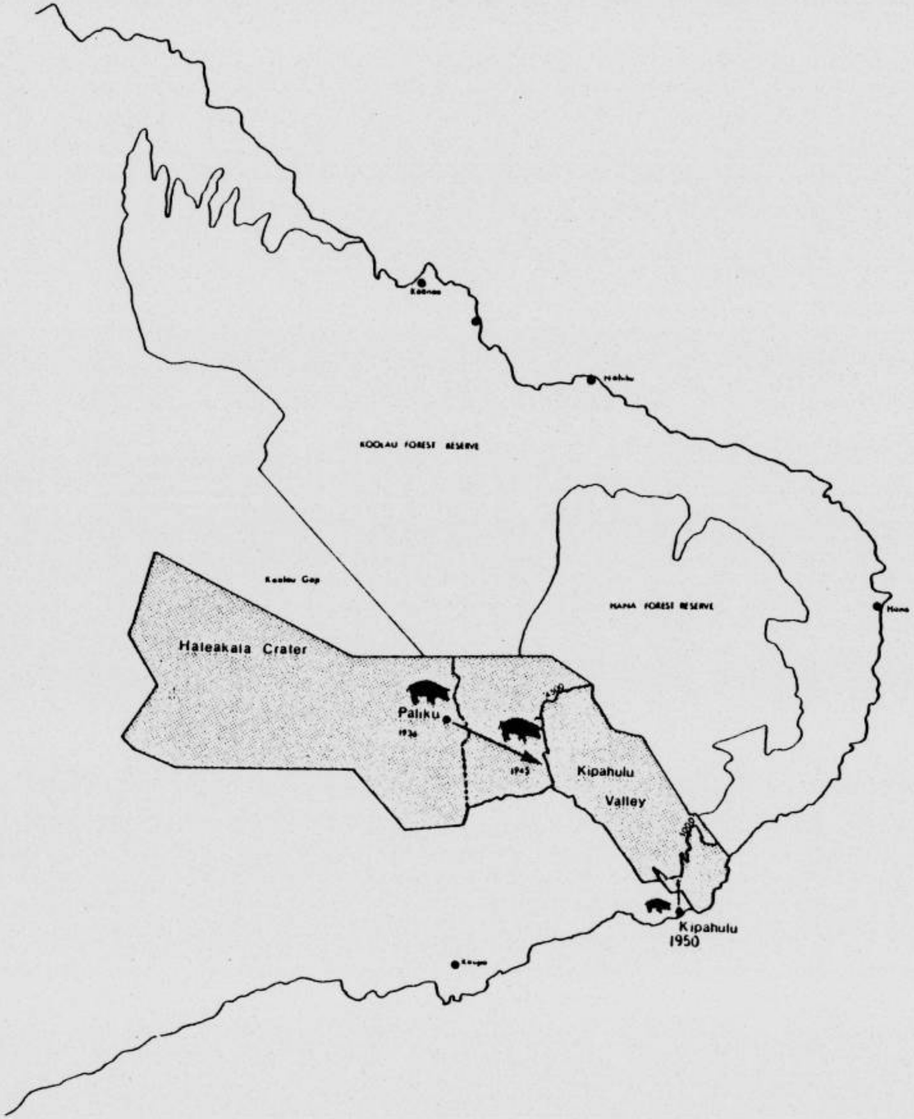
CHAPTER 4

FERAL HISTORY

Domestic animals that invade a habitat and establish breeding populations may be characterized in three ways: the length of time since escape from domestication, rate of invasion, and the genetic constitution of the founder population. Since introduced feral mammmals often undergo eruptive fluctuations (Riney 1964), a knowledge of the length of time a population has been in an area would facilitate evaluation of population and vegetation characteristics. Typically, invasion of new habitats is by dispersal of subadult and adult animals (Singer 1981). The rate of invasion is measured as the rate of increase of a linear dimension of the range (Caughley 1977). The size, age, sex and genetic composition of the founder population is usually not well documented, hence reliance on observations by competent naturalists and long-time residents has to be made. The interview approach was adopted in an attempt to trace the history of the population in the Valley. Interviews were conducted with long-time residents, pig and goat hunters from Kaupo, Kipahulu, Hana, Nahiku and members of the Maui Sporting Club, Makawao, Maui.

Pig invasion into Kipahulu Valley is a recent event and occurred first from Haleakala Crater and later from coastal Kipahulu (Figure 11). The Crater was apparently pig-free before the nineteenth century. In 1841, naturalists Pickering, Drayton and Brackenridge of the United States Exploring Expedition (Wilkes 1845), together with 13 local

Figure 11: Pig invasion into Kipahulu Valley, Haleakala National Park, Maui, Hawaii. Note that the Valley was invaded from two geographic fronts and at two different times. Diagram also shows the location of the Valley in relation to the surrounding areas.


Keanae
Nahiku
KOOLAU FOREST RESERVE
Koolau Gap
HANA FOREST RESERVE
Hana
Haleakala Crater
Paliku
1936
1945
4500
Kipahulu
Valley
1000
Kipahulu
1950
Kaupo

residents and missionaries, explored Haleakala Crater. No pigs were observed; the only mammals reported were two ungulates, goats and cattle, and a canid, the dog. In the early 1900s, goat hunting on Haleakala became an important sport. Until the 1930s no pig was ever observed by any regular Haleakala District goat hunter. In 1936, pigs were first sighted at Paliku (Freitas 1979 Makawao, Maui--taped interview) which is within the present Park boundary. Animals invading Haleakala District had white, black, red, and mixed coat colors, and were of domestic-type conformations. Polynesian-type pigs (Santos 1974 Kahului, Maui--taped interview) were not ("never seen one of those") encountered.

Pigs that were first seen in Haleakala District were believed to be derived from runaway domestic breeds in the Keanae and Piinau areas. Dispersal of feral populations from these areas into Haleakala District was believed to have proceeded from the north via Ainahou in the Koolau Gap. Hunting with dogs was singled out as an effective but dispersive method of harvesting pigs, and was claimed by one interviewee to be the factor that accelerated pig movements from lower areas into Haleakala District. Dog hunting in Haleakala District was however discontinued in 1961; the last two persons to dog-hunt on Haleakala were Frank Freitas and Anson Akoi.

Downhill movements of pigs from Haleakala Crater into the upper reaches of the Valley probably began as early as 1935. By 1945, signs of pig activity were observed in the head of the Valley down to 1370m (Fagerlund 1945, Hjort 1945). The Valley from 1370 to 610m was, however, pig-free and described by the two expedition members, Fagerlund and Hjort, as "virgin forest." In the same year, Jack Lind, a Kipahulu resident, penetrated the Valley's lower plateau from below and hiked up to "the bend" (ca. 730m) to check unconfirmed reports of feral cattle (Lind 1979 Kipahulu, Maui—taped interview). Lind, who saw no cattle or pigs, nor signs of these animals, described the rain forest as "virgin land." Hence the Valley below 1370m was essentially pig-free in 1945, and hill invasion by pigs from coastal Kipahulu was thus a post-1945 event.

Coastal Kipahulu, during the early 1900s, was an important agricultural and population center in Hana District. Here pigs were raised under confinement. Several breeder farms were in operation; those belonging to Hiram Apo, David Kaalakeaui, Paul Kaiwi Sr., Jack Lind, Kopai Starkay and Louis Smith, each housed 20-30 sows. Whereas breeder sows were confined, their litters were not; they were allowed to run freely and were raised in open pasture, under what was then known as free-farming (Lind 1979—taped interview). Free-farming appears to be the only system by which early Hawaiians and Polynesians could maintain a steady supply of animal protein. When confinement methods for raising pigs became mandatory on some Pacific islands for health reasons, pork production declined or stopped altogether (Luomala 1962). Natives were unable or unwilling to raise enough crops to feed the pigs.

Free-farming of pigs in coastal Kipahulu, practiced with the underlying principle of maximum pork at minimum cost and encouraged by the then Department of Agriculture (Hollingsworth 1853), was in addition to confinement rearing, a widely-practiced mode of pig husbandry in Kipahulu and Kaupo. Litters born in open pasture and raised by the sow herself were known to associate to a lesser extent with the general domestic herd. States of existence in pigs raised by free-farming including those that have escaped were essentially of domestic-pariah and pariah forms, as borne out by such descriptions: "they *sometimes* come back to feed," and "we *know* where they are," (emphases are mine). Upslope invasion of the Valley by domestic breeds from coastal Kipahulu thus began with free-farming practices, which led to the formation of pariah populations and feralization of pigs via the pariah population model.

A food resource which might have been of importance in encouraging pariah states of existence and holding initial feral population to lower elevations was the strawberry guava, *Psidium cattleianum*. This exotic plant was already established in Kipahulu pastureland and lower Kipahulu Valley prior to the uphill feralization of pigs into the Valley. By 1950, true feral populations were found on Palikea and adjacent areas. In the early 1960s, some 10 years after their feralization, pigs were described as being very abundant on Palikea, Puu Ahuula, and from the coast in upper pastureland and lower Kipahulu Valley. Pig hunting for table meat and trophies became important and popular at this time when breeder farms were no longer in operation. Hunting dogs were raised and special breeds were kept. At least 200 pigs were harvested annually by two Kipahulu families from Kipahulu pastureland and the lower Valley. Upslope hunting with dogs was believed to have accelerated pig movements up the Valley, initially at least. Pigs had probably invaded the entire Valley well before 1967, but it was in that year that the occupation of the entire Valley by pigs was first documented by scientists (Warner 1967).

Thus the Valley was invaded along two geographic fronts, at two different times and with two sources of animals which appeared genetically similar, i.e. European domestic breeds. The present Valley populaton has been in existence for about 30-35 years.

The minimum rate of invasion was 0.45km per year, assuming complete occupation of the Valley by pigs in 1967 and that the invasion front at 1370m was reached by pigs from coastal Kipahulu. A more realistic rate of spread would be 0.76km per year. Rates of invasion may be atypical because of the bounded palis, which by restricting lateral dispersal could have inadvertently increased dispersal in the upslope direction. Caution must be observed when rates of spread are to be compared between studies. That published for feral pigs in forest-scrubland-grassland-mountainous terrain on Auckland Island, New Zealand is 0.67km per year (Challies 1975). The wild boar in the mountainous deciduous forest in Great Smoky Mountains National Park was found to spread at a rate of 2.75km per year. Although cited references are not very explicit, it is most likely that the maximum rates of invasion are given. The rate of spread for the pigs in the highly dissected Valley and the relatively short period of time the animal took to occupy the area shows its ability to disperse over rough terrain and that the gait and travel patterns in this quadruped are adapted for movements in difficult terrain.

CHAPTER 5

DESCRIPTION OF THE ANIMAL

Throughout its geographic range, the feral pig shows marked differences in external morphology. Description of physical characteristics in the Kipahulu Valley population at this point in its feral existence is thus appropriate. Pigs in this population are compared with those in other insular habitats. Attempts are made to account for measurable interpopulation differences in body conformation.

Physical Characteristics

The Kipahulu population is characterized by an admixture of traits of modern domestic breeds. Tamworth and Yorkshire types were easily identifiable. Despite claims by Kipahulu hunters that the aboriginal Polynesian pig was at least until recently sighted in the Valley, no such animals were observed during the 60 man-months of fieldwork.

Feral pigs in Kipahulu Valley had visibly recognizable domestic body conformations and features (Figure 12). The head was relatively short in relation to total body length. The profile of the snout was slightly concave, and nasal plates were broad, highly tactile and well developed. Ears ranged in size from medium to large, were flexible, were affixed more or less perpendicular to the head or inclined forwards and thus did not rest alongside the back of the head. This domestic ear carriage differed from that in "mountain pigs" of Hawaii (Giffin 1978) or in the Asiatic wild boar (Diong 1973). Shoulders were not

Figure 12: Feral pigs in Kipahulu Valley. (a) Two sows in a strawberry guava (Psidium cattleianum) forest at E700m. Note the pronounced domestic features and the sway-back character in the black-coated pig. See text for description. (b) A white and spotted pig in a dense fern (Athyrium sp.) cover at L850m.

a

b

disproportionately higher than the hind quarters. Shoulder shields found in "mountain pigs" and the wild boar were absent. The dorsum of the body in the standing animal was usually horizontal with the ground, except in arched-back animals (Figure 12) which probably represented the Chinese breed. In these animals the abdomen barely cleared the ground and the skin between the eyes was somewhat wrinkled. Most pigs in Kipahulu Valley had compact, barrel-shaped bodies. Long-bodied red animals had relatively short legs, and in lactating animals of this type, the nipples almost trailed the ground. The tail was usually straight. Small-sized animals with long, straight, pointed snouts and smaller nasal plates were uncommon and probably were an admixture of Tamworths and other breed types. Tamworths are known to have long, straight snouts (Fradrich 1972). Meat color (redness) and texture from pigs in the Valley resemble the meats in pen-raised domestic pigs more than do meats of feral pigs from the Kaupo and Nahiku areas, probably because of strongly residual domestic breed genes, food habits and later history of feral existence in the Valley population.

Anomalies

Umbilical hernia was observed once only, in a seemingly healthy, nonparous, six-month old sow shot by a hunter at K800m. An abdominal protrusion ball at necropsy showed a prominent subdermal hernia of the small intestine through the imperfectly closed navel. This nonlethal condition is believed to be a hereditary weakening of the umbilical musculature (Pond and Houpt 1978). Violent exertion, jumping and forcible expulsion of urine and feces through obstructed passages could also predispose an animal to hernia. This single observation suggests a low incidence of the defect or a poor survival of herniated pigs in the wild.

Varying degrees of ear anomalies (Figure 13) were observed in six animals. Three pigs had stumpy microtial ears (Figure 13a) where auricles were multi-lobed and reduced to less than 3cm. The margins of the auricular lobes were haired and the skin did not appear to be scarred. Two animals had accessory ear lobes, abnormal concha curvature and irregular skin folds and protuberances at the bases of the ears. Observed anomalies appeared similar to the congenital ear defects in domestic pigs described and illustrated in Plate 4 of Nordby (1929). Additionally, the external auditory meatus were either partially or completely occluded in these animals. They frequently cocked their heads when alert to sounds, suggesting probable hearing impairment. Two other pigs had asymmetrical anotial anomalies (Figure 13b), and no ear canals. An extreme case of earlessness was observed in a boar (Figure 13c). This animal, observed for a period of 10 minutes, did not respond to gun fire or other sounds and, in my judgment, was deaf. Necropsy revealed complete decanalization of both external auditory meati and a 2cm wide band of white, shiny, hairless skin arched over the top and sides of the neck. The right eye was normal, but the left eye structure was absent.

Ear anomalies may be an intrapopulation phenomenon, but two other possibilities need to be considered. Split ears (Annett 1938) and other congenital ear defects (Nordby 1929) have been documented in domestic

Figure 13: Examples of ear abnormalities in feral pigs in Kipahulu Valley, Maui. (a) Microtial ears in a sow trapped in E5, (b) Right ear anotia in a boar observed at E700m, (c) Symmetrical anotia (earlessness) in a boar observed at L750m. See text for description of these and other associated ear abnormalities.

a

b

c

pigs. Nutrition, in-breeding, disease during pregnancy and unfavorable environmental conditions are among the causes of congenital ear or eye defects in domestic pigs (Mellen 1959, Pond and Houpt 1978). In the wild, congenital defects might act to check numbers in a population from below. Ear anomaly was however not found in 20 groups of fetuses, and thus suggests the observed anomalies could have been produced by extrinsic factors. Kipahulu hunters were known to mark dog-caught piglets by ear slicing or castration. No barrows were seen and it was very unlikely that ear anomalies were man-imposed. Earlessness in the 26-month boar in Figure 14c could have been due to chronic snare or rope burns, although snaring was not used in the Valley during the last three years. Another possibility is that the ears might have been mutilated or removed by feral dogs or mongooses whose role as a predator had been established in this study. Trauma, inflammation otitis externa (Palumbo 1981 - pers. comm.), could occlude the ear canals.

Weights and Body Measurements

Weights were recorded to the nearest 5 pounds using a 300 pound capacity Viking scale (Forestry Supplies, Mississippi) and later converted to metric. A pulley was used to hoist animals for weighing. A total of 22 trapped animals were weighed and measured. Age was estimated to the nearest month using dental features (Matschke 1967). Body measurements and the classification of weighed animals into broad age classes were after Giffin (1978). This procedure was adopted to allow comparison of growth parameters with feral pigs in other similar habitats.

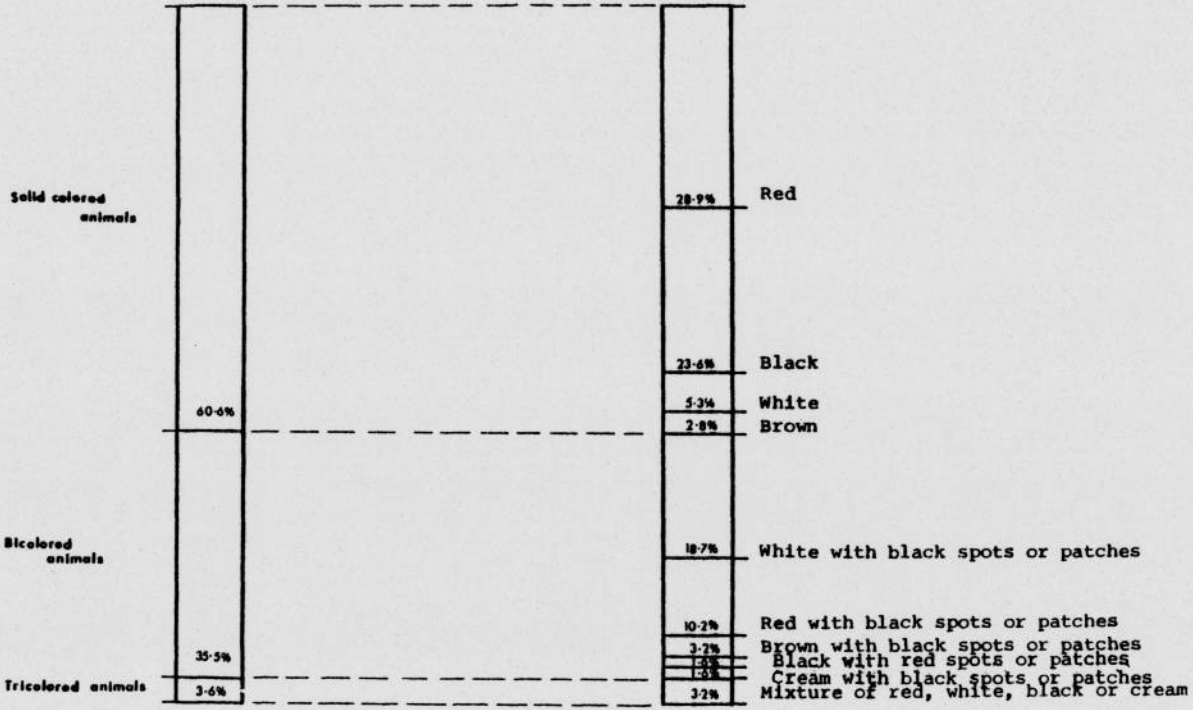


Figure 14: Coat color classes and compositions of feral pigs in Kipahulu Valley, Maui, Hawaii. In bi- and tricolored animals, the first mentionted color represents the dominant coat color. Sample size based on total number of trapped (94), shot (34) and sighted (117) animals.

Average weight and body measurements (Table 7) were comparable to feral pigs in rain forest habitats on the island of Hawaii (Giffin 1978) but, as expected, were considerably higher than average weights for "mountain pigs" on Mauna Kea. The average weight for animals older than one year was 59kg (N = 22). The heaviest pig weighed 102kg, had a total length of 145cm, head length of 38cm and a chest girth of 106cm. Field observations indicated that body length was correlated with weight in long-bodied animals, while chest girth was correlated with weight in compact barrel-shaped animals. Brisbin et al. (1977) reported on the high correlation between length and weight of individual pigs in two feral populations in southeastern United States. Barrett (1978) observed that chest girth, a reversible growth parameter, was a reliable weight correlate for feral pigs.

Coat Color Composition

Pigs were generally densely covered with hair. Coats in piglets were well developed *in utero* during their third trimester; thus, piglets were fully haired at birth. Long-bodied red pigs and black pigs with arched backs generally had sparser and shorter hair. The mid-dorsal mane was present in 85.1% of trapped animals, and was usually more prominent in piebald and black animals. Spinal hairs located just posterior to the head were bristle-like, erectile, commonly split terminally and thickest and longest of all hairs on the body.

TABLE 7 : Weights and body measurements for 22 feral pigs in Kipahulu Valley.

Age (months)	N	Sex	Weight (kg)	Head length (mm)	Total length (mm)	Ear length (mm)	Chest girth (mm)
8 - 12	2	M	30 (25-34)	201 (198-225)	745 (705- 785)	99 (93-106)	550 (520-580)
	1	F	32	260	1010	13	720
12 - 14	2	M	50 (32-68)	275 (260-290)	1276 (1238-1315)	115 (100-130)	690 (660-720)
	4	F	47 (34-66)	262 (240-280)	1202 (1080-1345)	124 (102-142)	735 (700-790)
14 - 18	3	M	47 (39-57)	294 (282-304)	1262 (1182-1380)	132 (121-142)	811 (756-848)
	2	F	43 (36-50)	281 (273-290)	1300 (1250-1350)	141 (132-150)	769 (742-797)
20 - 24	2*	M	60 (50-70)	332 (320-345)	1421 (1374-1467)	140 (135-145)	840 (830-850)
	3	F	62 (50-73)	294 (275-320)	1461 (1420-1505)	138 (136-141)	824 (798-840)
25 - 36	2	M	73 (61-84)	345 (335-355)	1450 (1402-1498)	151 (148-154)	956 (938-975)
	2*	F	68 (64-73)	327 (320-335)	1520 (1480-1560)	131 (128-135)	871 (845-898)
36 - 42	2	M	76 (64-89)	350 (340-360)	1465 (1390-1540)	140 (136-144)	942 (900-985)
	1	F	102	380	1540	15	104

* Weight in these animals were estimated from chest measurements.

Four basic coat colors (black, red, white, and brown) and 10 pelage patterns were recognized (Figure 14). Solid white and cherry-red pelage stood out most outstandingly in the rain forest and solid red was the most common pelage pattern. The proportion of light-coated (non-black) to solid black-coated animals was 3.2:1. There were more solid colored animals than bicolored (spotted) animals. Among the solid colored animals, there were more red ($X^2 = 42.13$, $P<0.001$) than black-coated animals; the proportion of white-coated pigs was higher ($X^2 = 40.35$, $P<0.001$) than brown animals. Black included more common dull black, shiny coal black and the less frequently encountered agouti phenotype. Red coats were expressed in three shades; deep cherry red, red and dull red. All shades of red had been observed to occur together in single litters. White coat with black spots or patches (piebald) was the most common pelage in bi-colored animals. Pelages of tricolored animals were made up of a mixture of red, black, and cream or white. Belted animals were never observed.

Striped pelage was observed in a total of 12 piglets. This distinctly wild-type juvenile pelage was formed by six yellowish-brown stripes streaked length-wise, three on either side of the body. Stripes were usually continuous, and bright colored, but appeared indistinct and broken in a few animals. Juveniles two-months old still carried the striped pelage. This juvenile coat is normally lost at three to four months old.

A 2x6 chi-square analysis showed no significant difference (X^2 = 6.02, df = 5, P>0.25) in the frequency of coat colors in koa (610-1160m) and ohia forests (1220-1590m). A similar analysis, but using only trapped and shot animals, showed no significant difference (X^2 = 5.07, df = 5, P>0.25) in the frequency of coat colors between the sexes. Comparisons of coat colors in the upper and lower plateaus showed a significant difference (X^2 = 11.07, df = 5, P<0.001) in the frequencies of coat color distribution between the plateaus (Table 8). Red pelage as more common on the upper plateau while white was more so on the lower plateau. Omitting white from the contingency table, a recalculation of the chi-square contingency analysis showed that there was no significant difference (X^2 = 9.06, df = 4, P<0.10) in the frequencies of pelage patterns on both plateaus. A 2x2 contingency table comparing white and nonwhite showed a significant difference (X^2 = 21.24, df = 1, P<0.001) in this comparison. Thus among the basic coat colors, white occurred in the lower plateau with a relatively higher frequency than the other coat colors.

Discussion

The pig population in Kipahulu Valley resembles feral populations in rain forests on the island of Hawaii, but differs from feral populations in other insular habitats. Populations on Mauna Kea (MKP), Hawaii consist of small-sized pigs with long, pointed snouts, small erect ears, predominantly black coats, heavily bristled and undercoated with woolly hairs, high shoulders with thick shoulder shields, and long legs (Giffin 1978). Populations on Mona Island (MIP), Puerto Rico

TABLE 8: Coat color composition of feral pigs in the upper and lower plateaus of Kipahulu Valley.

Plateau	Coat color						
	Black	Red	Brown	White	Bicolored	Tricolored	Total[1]
Upper	42	61	5	2	67	4	181
	(72.4)[2]	(85.9)	(71.4)	(15.3)	(77.0)	(44.4)	
Lower	16	10	2	11	20	5	64
	(27.5)	(14.1)	(28.5)	(84.6)	(22.9)	(55.5)	
Both plateaus	58	71	7	13	87	9	245

[1] Sample size based on trapped, shot, and sighted animals.
[2] Percent color composition on plateaus.

(Wiewandt 1977) have long snouts, long legs, small ears, are without a dorsal mane, and average total length and weight lower than KVP pigs. The Ossabaw Island, Georgia, population (OIP) (Brisbin et al. 1977) has average body lengths and weights respectively shorter and lower than the Valley pigs. Feral pigs on Guam, Marianas Islands (GP) are relatively small-sized (Kami et al. 1976) have small ears and long snouts. Feral populations on Kangaroo Island, Australia, (KIP) have short stature and approached the size of miniature pigs (McIntosh & Pointon 1981). The Galapagos Islands populations (GIP) have long legs, long snouts, small erect ears but possess domestic coat patterns (Kruska & Rohrs 1974).

There are several reasons for the differences between the Valley pigs and those in other areas. Kipahulu Valley pigs have a late feral history (30 years) and is comparable in length of feral existence to the continental population in Savannah River Plant (SRP), Georgia (25 years), but is considerably more recent than pigs in the MKP (ca. 1200 years), OIP (several hundred years), GIP (70 to 140 years), MIP (about 384 years), GP (>700 years) and KIP (ca. 180 years). Since feralization re-exposes a population's gene pool to natural selection, older populations are likely more intensively selected for adaptable traits than in more recent (SRP) populations. Pigs with longer feral histories appear to be small-sized and black-coated, resembling ancestral wild stock. Pigs in SRP are comparable in size and body conformation to pigs in the Valley, but are larger, as is the case in Kipahulu Valley, than pigs in other insular populations. The Ossabaw Island population and KIP, derived from European domestic breeds and with more than a century of feral history, have evolved into smaller-sized animals well adapted for the respective habitats. KIP is unique in that a new race with body size approaching that of a miniature pig has evolved. Small size may be selectively more advantageous than large size in less favorable environments. The daily energy requirements are less for small than large-sized pigs (Asahi 1975). Food availability may affect body size. The nutritional plane of pigs in the Valley appears to be higher than in other populations. Staple foods of pigs in the Valley are characterized by high nitrogen-free extract (Chapter 6), whereas foods of pigs in MKP, as can be inferred from Giffin (1978), are high in crude fiber. Dietary protein in the form of earthworms is probably much less available, on a per unit search effort basis, to pigs in the more arid and seasonal mountain pasture habitats than to pigs in the high rainfall, nonseasonal population in Kipahulu Valley.

The gene pool of the founding animals could probably account for some of the differences in physical characteristics among the several populations. MKP was believed to be descended from "early type" (Polynesian breed) pigs. GP was thought to be derived from the small-sized Neapolitan pig, S. s. meridionalis. GIP and MIP were founded by early-type primitive breeds released on the islands by marines. Pigs in all four insular populations share similar physical characteristics: black pelage, small size, long snout, long legs, short erect ears, and resemblance to the wild ancestor. As explained in Chapter 2, primitive or early-type pigs are smaller, long-snouted, and ancestral in appearance because they are in an early stage of domestication. Populations founded by more primitive genomes and subsequently isolated geographically or insularly would therefore have their ancestral characters reinforced, until such time as modern domestic blood-lines enter the population.

Unlike all the other populations, KVP was founded by modern domestic breeds, In the early 1900s ranchers introduced Tamworths, Berkshires, Durocs, and Hampshires into the islands as breeding stock for herd improvement. These breeds were raised in the breeder farms in Kipahulu, and together with other domestic breeds (e.g., Yorkshire) formed the gene pool of the founding popultion. Thus, KVP differs from most other insular populations in that the genetic pool of the founders was made up of improved modern domestic breeds.

Black (gray, agouti) is the ancestral coat color. This pelage seems to characterize older populations, but not the KVP. Since it has been observed that older populations were founded on early-type genomes, it follows that black would be the most common color phenotype in such populations. A commonly held view is that when pigs revert from domestic to feral states of existence, their variously colored domestic coats revert in time to black. However, some colors may be selectively more advantageous than others in some habitat. Pigs on Haleakala Crater District, Maui, and alpine habitats on Hawaii are predominantly black-coated. Light colored animals are rare on Mauna Kea; white coated animals are absent (Giffin 1978).

Dark coats absorb short wave-length light more effectively and hence insulate the animals better than light colored coats (Finch 1980). Black would appear to have a selective advantage over other coat colors in more extreme alpine habitats. The high frequency of light-coated animals in KVP contrasts with that for feral pigs in rain forests on Hawaii, where black appears to be the dominant (N = 48) pelage (Giffin 1978). White-coated pigs are susceptible to sun scalding (Hetzer 1945). The absence of white coats in OIP, despite known release of white boars, has been attributed to natural selection (Brisbin et al. 1977) which is possible as pigs in OIP had to feed in open marshes where sunscalding might be severe. White is a dominant genetic character (Hetzer 1945) and was fairly well represented on the lower plateau of KVP where it is less likely to be selected against in the closed canopy rain forest.

Despite a late feral history, the Valley pigs have adjusted well to an existence in the rain forest. The domestic conformation and large body size in this population is probably maintained by the abundance of food and the improved modern domestic genome upon which it was founded. However, it is tempting to hypothesize that, in time, undisturbed feral existence in this enclave, through inbreeding and food depletion, may produce smaller-sized animals and further modification of the present domestic body conformation.

CHAPTER 6

FOOD AND FEEDING HABITS

Introduction

Food is central in the study of animal populations. Quantity and quality of foods are primary determinants of animal numbers, growth and distribution. Hence, animals exercise nutritional choice by optimizing their activities so that the "right kind of food" is searched for and "enough of it" is eaten (Elton 1966). By selecting their foods, animals control the transfer of biomass between trophic levels, affect ecosystem functions and in turn are influenced by changes within the ecosystem. Food habit studies will, therefore, enhance the understanding of population processes, ecological relationships and community interactions and contribute to better management of natural resources and animal populations.

Food habits of feral pigs have been investigated in a wide range of habitats: oak-sedge flats (Springer 1977); desert scrub and managed pastureland (Barrett 1978); pine forest, salt and freshwater marshes (Brisbin 1974; Wood & Roark 1980); mountainous forest, scrub and grassland (Challies 1975; Rudge 1976); and alpine grassland and rain forest (Giffin 1978). These studies have shown food preferences in pigs, seasonal variation in diets, relationships between food availability and reproduction, and in some instances, food competition with other wildlife. Practically all food habit studies of pigs show that diets and foraging habits alter plant communities and damage natural ecosystems.

Feral pigs in the evergreen montane rain forests in the Hawaiian islands appear to be surrounded by a surfeit of food throughout the year. That food supply could limit numbers in this habitat seemed unlikely. However, some plants are poor foods because of nutrient dilution, particularly of available nitrogen (White 1978). Nutritionally, therefore, all that is green need not be utilizable or sufficient for animals. Food which contains enough nitrogen is particularly important for the survival of young; the relative shortage of nitrogenous food is probably the single most important factor limiting the abundance of pigs in some habitats (Barrett 1978; White 1978). The abundance of feral pigs in rain forest environments may be controlled from below by the availability of foods rich in dietary protein. This hypothesis was examined by studying the pig's diet, food preferences, nutrient quality of plant foods and evaluating blood biochemical values (Chapter 10) that are reliable correlates of nutritional status. Additionally, it was also the intent of this study to evaluate the effects of the pig's food habits on the rain forest ecosystem.

Materials and Methods

Diets and feeding habits were studied by four methods. Whenever possible, feeding activities were observed during all encounters with animals. Preference for the strawberry guava was investigated by examining fresh scats found along the central escarpment trail from September to December of 1978, and throughout 1980. Scats visibly loaded with strawberry guava seeds were not collected but their elevations were recorded; those that did not appear to contain the seeds were collected and later flushed through a size 3 Newark sieve to collect strawberry guava seeds. Attempts were made to determine diets by microscopic examination of fecal materials. Amorphous and fragmentary fecal materials on the sieve and collecting pan were preserved in formalin and later pipetted to a slide for microscopic examination. Freshly abandoned feeding sites, when located, were examined for foods selected, parts eaten or rejected and general feeding behavior and stomach contents analyzed to determine the general diet.

Pigs were shot each month for stomach analysis. The degree of stomach fullness at increments of 25%, and the time of shooting, were noted. Stomachs were preserved in 10% formalin for later analysis in the laboratory. Food items were sorted visually into the following general categories: tree fern core, grasses, sedges, fruits, bark, leaves, roots, animal matter and unknowns. Plant foods within each category were identified as far as possible. The presence of each identifiable food item in a stomach was recorded as a percentage occurrence. Percentage frequency was calculated as the proportion of the number of stomachs that contained a particular food item to the total number of stomachs, multiplied by 100. Volume of each food category was determined volumetrically either by water displacement or direct measurement (e.g. tree fern core) with a graduated cylinder.

Total volume of the ingesta for each stomach was determined by summing individual volume of each food category and unknowns. Percentage volume composition was calculated as the proportion of the volume occupied by a food item to the aggregate volume (Martin et al. 1946) of contents, multiplied by 100. Importance values (McCaffery et al. 1974) for overall and seasonal major food categories were determined by calculating the index: percent composition x percent frequency in the diet.

Nutritive values of plant foods were determined by subjecting composite samples of plant parts known to be eaten by pigs to proximate analyses using A.O.A.C. (1975) methods. Plant fractions analyzed were dry matter, crude protein, ether extract, crude fiber and ash. Mineral compositions were determined by X-ray fluorescence on a quantometer (Applied Research Laboratory, California). All volumes, except those for ash, were expressed on both dry and organic matter bases.

Results

(a) Stomach fullness

Diets of 28 pigs (6-60 months) were determined by examining stomach contents of 12 male and 16 female animals. Twenty-one of these animals were from the upper plateau koa forest (600 to 1190m), six were from ohia forest (1190 to 1520m), and one was from the lower plateau (730m). Stomach collection was biased towards older animals because larger pigs were preferentially shot.

A plot of individual stomach volume against dental age shows a wide scatter (Fig. 15). The median stomach volume was 3.2 liters; the largest sample measured 4.482 liters. Food items were present in all 28 stomachs; 20 were classed as full stomachs, 4 were 75% full, 2 were 50% full, and one was 25% filled. Although all samples were collected during daylight hours, from 0600 to 1800 hours, the distribution of full stomachs grouped over four three-hourly intervals, was uniform throughout the day (Kolmogrov-Smirnov test $D = 0.10$, $P < 0.50$). In full stomachs, food items were not well mixed. Ingesta from the last meal showed a marked layering pattern, with more recent ingesta layered from the cardiac to the pyloric end of the stomach. Ingesta layering was most pronounced in diets consisting of ferns, roots, graminids (grasses and sedges) or leafy vegetation, but was not at all apparent in half-filled stomachs, and in those where strawberry guava was the principal dietary item.

(b) Overall dietary composition

Plant matter constitutes over 90% of the diet of pigs in the rain forest (Table 9). Animal matter had a frequency of 89.2% (N=28) occurrence and was represented principally by oligochaetes and native land snails. Arthropods occurred as traces (less than 0.1%). Based on stomach analysis, 31 plant foods were identified (Tables 9, 10, 11). This dietary range was made up of 22 native plants and nine exotic species. Ten other plants, not encountered in stomach content analyses, were ascertained as forage from field observations. Thus, the dietary

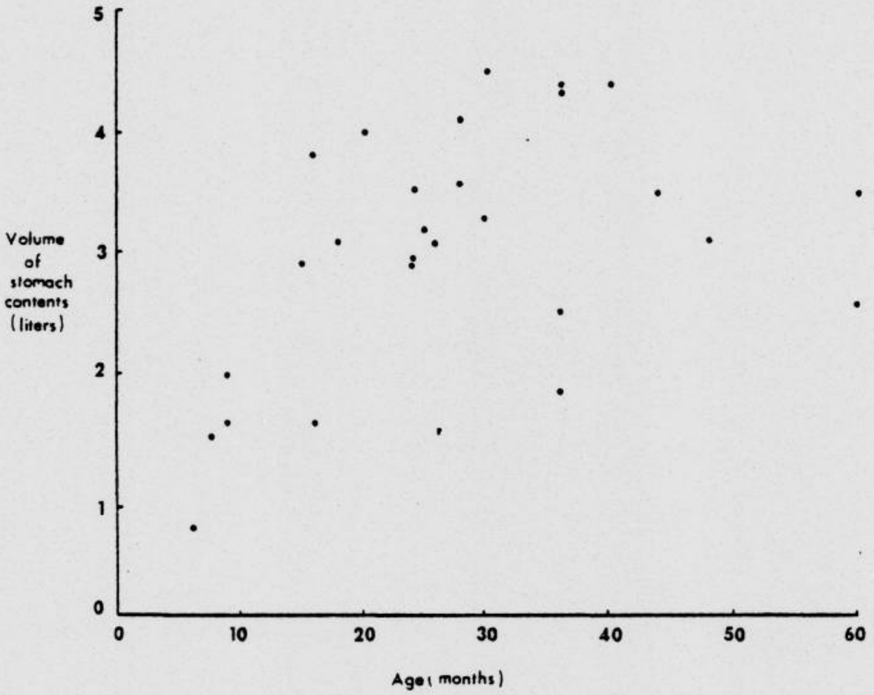


Figure 15: Plot of individual stomach volume against age for 28 feral pigs shot in Kipahulu Valley between 610 and 1500m.

TABLE 9: Overall annual percentage composition (aggregate volume), occurrence and importance values of major food categories for feral pigs in koa and ohia forests in Kipahulu Valley, as revealed by analyses of 28 stomachs.

Food category			Percent occurrence[1]	Percent of aggregate volume	Importance value[2]
Plant matter					
Cibotium sp.			71.4	42.7	3049
Psidium cattleianum			57.1	28.4	1622
Freycinetia arborea			39.2	5.6	220
Leaves	*Broussaisia arguta*	57.1	60.7	2.5	152
	Acacia koa	28.5			
	Cheirodendron trigynum	50.0			
	Hydrocotyl sp.	28.5			
	Eupatorium sp.	21.4			
	Pepperomia sp.	7.1			
Bark	*Clermontia* sp.	32.1	32.1	3.2	102
	Cordyline terminalis	7.1			
	Others	21.4			
Roots	*Astelia* sp.	17.8	32.1	3.1	100
	Others	17.8			
Athyrium sp.			60.7	1.4	85
Grasses	*Paspalum conjugatum*	28.5	32.1	2.1	67
	Others	7.1			
Sedges	*Carex alligata*	21.4	25.0	1.4	35
	Uncinia uncinata	3.5			
	Machaerina sp.	14.2			
	Cyperus sp.	17.8			
Animal matter					
Earthworm			89.2	6.2	553
Molluscs			10.7	0.4	1

[1] Percentage of stomachs containing a particular food category.

[2] Percent volume x percent frequency occurrence; rounded to the nearest whole integer.

Unknowns, traces and amorphous materials make up the rest of the percent volume.

range comprised of at least 40 plant foods. The botanical composition of the overall forage was 62.5% (25) herbaceous plants, 32.5% (14) trees, and one woody vine. Seventy percent (28) of the pig's forage were native plants, and of these 85.7% (24) were endemics. Thus, food habits of the feral pigs were characterized by a wide dietary range and forage which was comprised essentially of herbaceous natives.

Overall food preferences showed that four plant foods, tree fern (*Cibotium* sp.) core, strawberry guava (*Psidium cattleianum*), woody vine (*Freycinetia arborea*) and tree bark made up 80% of the diet (Table 9). Tree fern had the highest percentage occurrence and percent aggregate volume and thus formed the bulk of the diet volume. On an annual basis, percent aggregate volume for tree fern was higher than for strawberry guava. Unlike several other food items, tree fern core (13.3 to 91.5%) was never recorded as traces, suggesting a definite food preference as well as indicating the relative abundance of the food.

Importance values for all categories of plant foods ranked as follows: tree fern, strawberry guava, woody vine, leaves, bark roots, *Athyrium* sp. and sedges. When animal matter was included in the ranking, earthworms ranked third in food choice. Thus, the four most important year round foods on the basis of importance values were tree ferns, strawberry guava, earthworms and woody vine.

(c) Seasonal influence on diet in koa forest animals

Monthly variations in percentage compositions of major food categories in stomachs of pigs (N=22) shot in koa forest were estimated. Tree fern core was most abundant in the diet from January to August, but dropped in abundance from September to December when strawberry guava formed the bulk of the diet (Fig. 16). Strawberry guava was present in stomachs for eight months of the year. Mean aggregate percentage volume for this item in 7 stomachs collected from September to November was 78.3%; two stomachs each had strawberry guava in 93.7 and 98.9% composition. All other fruits occurred as traces; thimble berry (*Rubus rosaefolius*) in eight stomachs, ohelo berry (*Vaccinium* sp.) in four stomachs, akala berry (*R. hawaiiensis*) and kukui nut (*Aleurites moluccana*) in one stomach each. Roseapple fruits (*Eugenia jambos*), recorded in three stomachs, was probably underrepresented in percent volume and frequency. Field observations showed that roseapple fruits were readily eaten by pigs rooting in roseapple forest.

Other fern foods identified were *Athyrium* sp., *Dicranopteris* sp., and *Lycopodium*. The most commonly eaten grass was *P. conjugatum*. *Cyperus* sp. was the most commonly foraged sedge; *Machaerina* and *Carex alligata* were the other sedges eaten. Roots were mostly present in small amounts and were unidentifiable to species level. Tree bark was most frequently represented by *Clermontia* sp. Leafy items were mostly from herbaceous plants. *Acacia koa* leaves and whole seedlings occurred as traces in 8 of 22 (36.3%) stomachs.

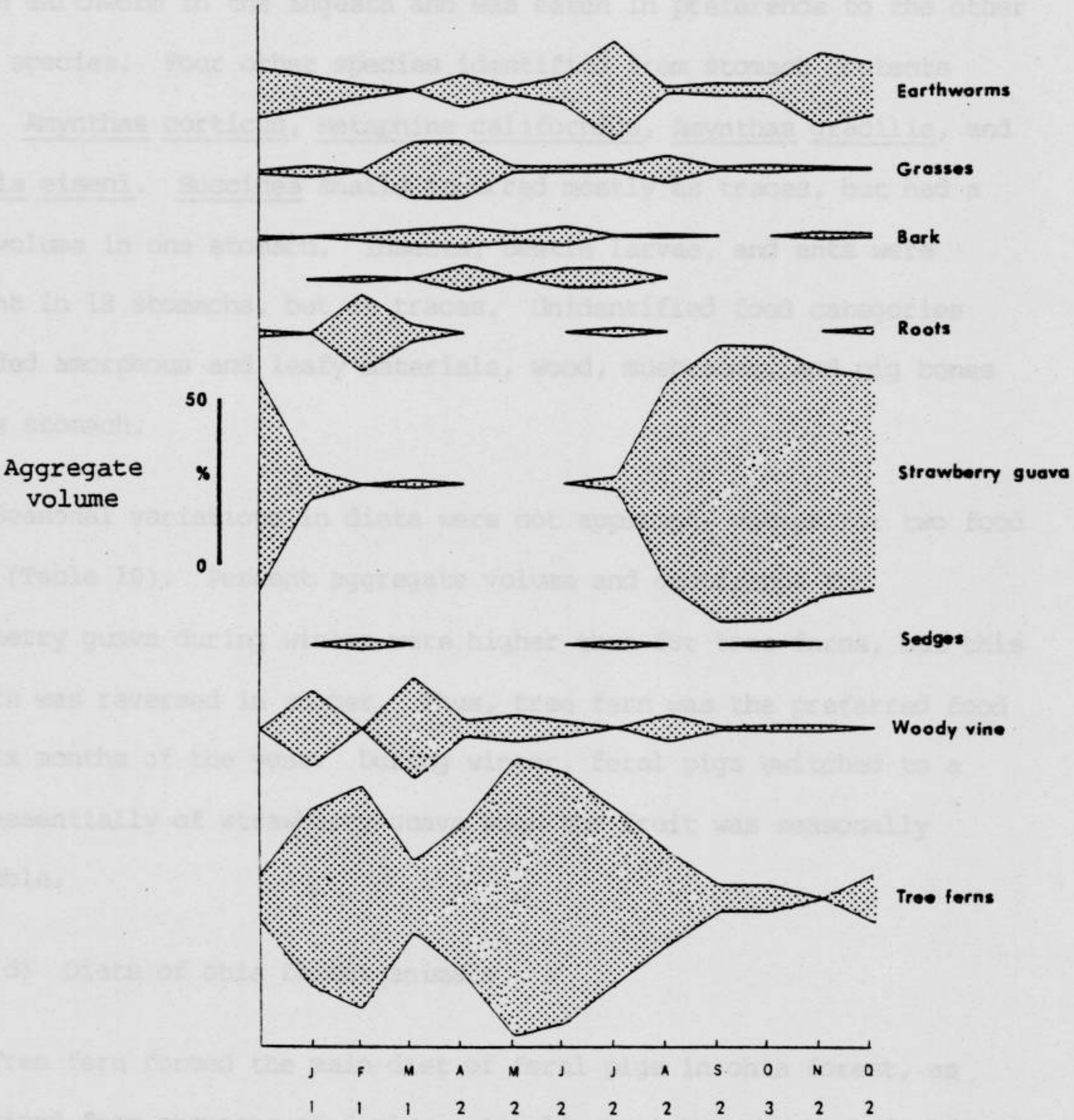


Figure 16: Monthly variations in percentage composition of major food categories as revealed by the analyses of 22 stomachs collected in the koa forest (610 to 1190m), Kipahulu Valley. Numerals below months indicate sample size.

Animal matter was dominated by earthworms. Over 90% of the stomachs contained earthworms; in one, earthworms constituted 29.3% (1018ml) of the total volume. Pontoscolex corethurus was the most common earthworm in the ingesta and was eaten in preference to the other eight species. Four other species identified from stomach contents were: Amynthas corticus, Metaphine californica, Amynthas gracilis, and Eisenia eiseni. Succinea snails occurred mostly as traces, but had a 2.3% volume in one stomach. Insects, beetle larvae, and ants were present in 18 stomachs, but as traces. Unidentified food categories included amorphous and leafy materials, wood, mushrooms, and pig bones in one stomach.

Seasonal variations in diets were not apparent, except for two food items (Table 10). Percent aggregate volume and occurrence for strawberry guava during winter were higher than for tree ferns, but this pattern was reversed in summer. Thus, tree fern was the preferred food for six months of the year. During winter, feral pigs switched to a diet essentially of strawberry guava when the fruit was seasonally available.

(d) Diets of ohia forest animals

Tree fern formed the main diet of feral pigs in ohia forest, as determined from stomachs of 6 pigs. Astelia sp., tree bark, and sedges occupied the second, third and fourth rank positions in food importance values (Table 11). Rank position for sedges in ohia forest animals were

TABLE 10: Seasonal variation in diets of feral pigs in koa forest (610 to 1190m), Kipahulu Valley.

Food category	Summer[1] (N = 10)		Winter[2] (N = 12)	
	Percent aggregate volume	Percent occurrence	Percent aggregate volume	Percent occurrence
Plant food				
Tree fern	52.5	80	27.9	50
Athyrium sp.	1.3	70	1.1	41.6
Woody vine	4.8	40	6.9	50
Grasses	0.6	30	4.2	50
Sedges	0.16	10	0.3	16.6
Roots	0.27	10	0.8	16.6
Strawberry guava	30.42	60	40.7	83.3
Leaves	2.1	40	1.9	66.6
Bark	1.6	30	0.8	25
Animal food				
Earthworms	4.46	90	9.7	91.6
Snails			0.7	8.3

[1] May to September

[2] October to April

TABLE 11: Average percentage composition of major food items in six stomachs collected from February to October 1980 in ohia forest (1180 - 1500m), Kipahulu Valley.

Food item		Percent composition[1]	Percent occurrence	Importance value
Plant food				
Tree ferns	*Cibotium* sp.	57.8	100	5780
Roots	*Astelia* sp.	8.2	83.3	683
Bark		10.8	50	540
Sedges	*Carex alligata*	5.5	66.6	392
	Uncinia uncinata	0.3	16.6	
Leaves	*Pepperomia* sp.	2.2	33.3	298
	Broussaisia arguta	2.2	33.3	
Athyrium sp.		2.5	83.3	208
Woody vine	*Freycinetia arborea*	4.2	16.6	70
Wood		0.5	33.3	17
Animal food		1.7	83.3	142
Earthworm		1.7	83.3	142
Land snails (*Succinea* sp.)		0.3	33.3	10

[1] Based on aggregate volume. *Dicranopteris* (fronds and stems), *Lycopodium*, *Hypochaeris radicata* (roots), *Vacinium* berries, *Cheirodendron* and *Metroisideros* leaves were present as traces. Unknowns, traces and amorphous materials make up the rest of the ingesta.

higher than in koa forest animals, but earthworms in ohia animals ranked lower than for pigs in koa forest.

(e) Diets of koa forest animals as revealed by scat analyses

Analyses of feral pig droppings for presence or absence of strawberry guava seeds showed that the proportion of scats containing the seed was both a function of elevation and seasons (Fig. 17). Proportion of droppings containing strawberry guava seeds was higher than at higher elevations, and higher during winter than summer seasons. No pig scats examined in ohia forest were positive for strawberry guava seed, the highest sighting of droppings containing the seed was at E945m.

(f) Foraging habits

Observations on foraging activities and freshly abandoned feeding sites provided additional information of the food habits of pigs. Feeding activities of feral pigs on 12 plant foods (Table 12) were watched for a total of about 180 min during the 30 months of field work. Most observations were brief and did not exceed one minute. There were two unusual sightings. On November 18, 1979, a group of five adult pigs at E640m was observed continuously for 55 minutes, from 1600 to 1655 hours. Another group of five animals, three adults and two juveniles at K700 was followed on June 10, 1980, within six meters, for 45 minutes from 0630 to 0715 hours. Feeding sites provided details of foods eaten, selected and those parts that were rejected.

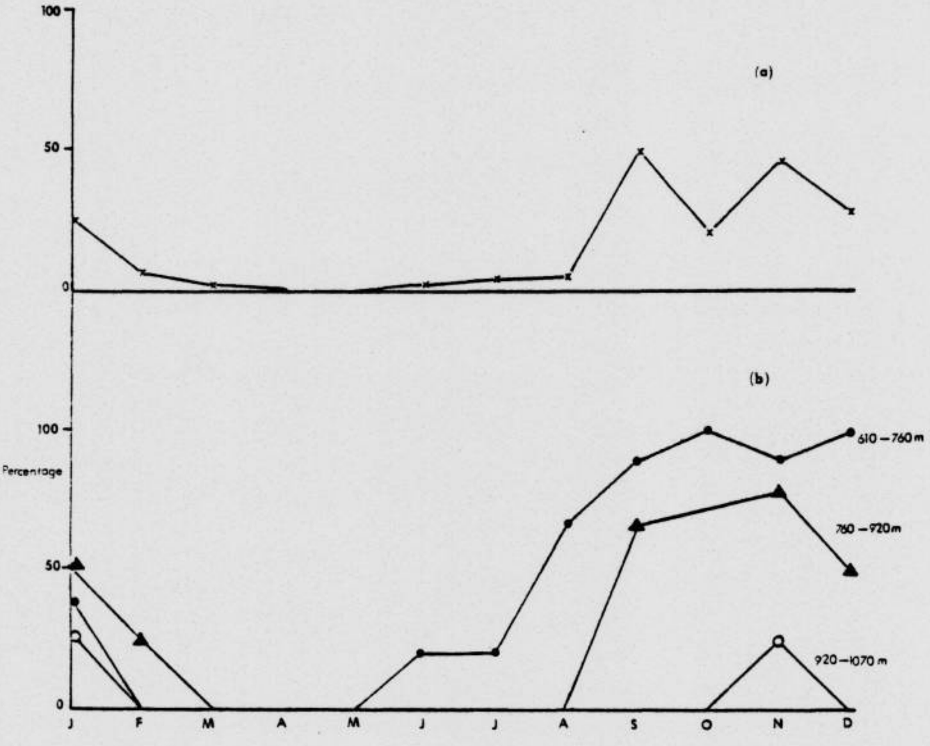


Figure 17: Monthly variation in the proportion of feral pig droppings containing seeds of <u>Psidium cattleianum</u>. Plots based on a total of 382 droppings examined along the central escarpment trail (610 to 1590m) in 1980. (a) all elevation (610 to 1590m) percentage plot, (b) percentage plot by elevation.

TABLE 12: Nutrient composition of plants eaten by feral pigs in Kipahulu Valley, Maui, Hawaii.

Plant foods	Parts eaten	Method of determination				Growth form	Chemical composition*						Mineral composition*								
		○	●	△	▲		DM	A	CP	EE	CF	NFE	P	K	Ca	Mg	Na	Mn	Fe	Cu	Zn
Acacia koa¯	S	+			+	T	26.1	4.4	21.6	3.0	24.6	46.4	0.11	0.75	0.40	0.22	0.50	233	583	5.0	44
Aleurites moluccana°	F	+				T	72.9	3.3	20.7	55.4	12.2	8.4	0.63	0.63	0.12	0.40	0.03	25	68	21.0	45
Astelia sp.¯	B/R	+			+	H	18.8	2.7	7.5	1.2	37.5	51.1	0.05	0.19	0.50	0.11	0.28	75	238	5.0	28
Athyrium sp.¯	yf/r	+		+	+	H	12.6	11.4	26.1	1.0	19.7	41.8	0.25	4.25	0.56	0.40	0.13	208	260	18.0	42
Broussaisia arguta¯	Sh/L	+			+	H	12.8	11.5	9.5	1.9	16.8	60.3	0.13	0.93	2.12	1.26	0.53	279	213	6.0	37
Carex arligata¯	L/s/I	+	+	+	+	H	29.0	3.9	8.4	1.4	38.1	48.2	0.09	1.11	0.11	0.12	0.28	320	131	9.5	40
Cheirodendron trigynum¯	L	+		+	+	t	21.3	9.2	10.6	5.6	23.7	50.9	0.13	1.98	1.36	0.42	0.43	960	65	4.0	51
Cibotium chamissoi¯	tc	+	+	+	+	t	32.4	2.3	5.1	0.3	9.1	83.2	0.08	0.50	0.21	0.09	0.07	34	26	9.0	26
	st/f	+		+	+		14.6	3.3	2.0	3.9	18.5	72.3	0.02	1.10	0.03	0.08	0.23	15	68	3.0	25
Clermontia sp.¯	b/L/Fl/F	+		+	+	t	11.8	7.9	6.6	7.7	22.6	55.2	0.07	0.29	0.70	0.27	1.93	250	350	5.0	61
Colocasia esculenta°	C				+	H	24.5	4.2	8.2	0.5	5.1	82.0	0.06	0.87	0.17	0.15	0.04	83	2450	3.5	43
Coprosma sp.¯	b				+	t	9.9	8.6	17.7	4.3	24.5	44.9	0.23	2.90	0.18	0.43	0.10	340	1005	6.0	75
Cordyline terminalis°	b	+			+	H	29.4	4.2	2.6	1.1	12.9	79.2	0.08	0.75	0.72	0.22	0.06	80	50	6.5	68
	L	+			+		21.1	5.9	10.3	2.8	25.6	55.4	0.20	1.58	0.56	0.47	0.04	147	60	8.0	73
Cyperus sp.‡	L/s	+			+	H	22.6	6.9	8.6	1.7	35.3	47.5	0.09	1.01	0.20	0.22	0.12	3458	308	3.0	48
Dicranopteris sp.†	f/s	+	+		+	H	20.2	3.6	11.0	3.0	28.9	53.5	0.11	1.12	0.06	0.10	0.06	327	53	5.5	25
Dubautia sp.¯	L/Fl	+			+	t	12.3	13.1	14.1	2.1	18.3	52.4	0.16	1.25	1.19	0.90	2.76	280	98	14.0	40
Eugenia jambois‡	F	+			+	t	14.7	2.5	3.9	5.8	9.1	78.7	0.06	0.63	0.28	0.18	0.04	12	64	5.0	60
Eupatorium adenophorum‡	L/s	+		+	+	H	11.8	10.3	18.3	7.6	12.2	51.6	0.19	2.25	1.07	0.64	0.07	470	140	29.0	100
Freycinetia arborea¯	Sh	+	+		+	wv	13.6	11.1	7.8	0.9	33.8	46.4	0.09	1.03	2.34	0.53	0.83	302	28	40.0	32
Gouldia hillebrandii¯	b			+	+	t	17.5	6.4	6.2	1.0	21.6	64.8	0.08	0.27	1.05	0.24	0.90.	710	209	11.0	54
Hydrocotyle verticillata‡	L	+		+	+	H	6.7	16.5	19.1	5.7	15.2	43.5	0.22	3.13	1.47	0.51	0.85	2660	4200	11.5	148
Lycopodium sp.†	WP	+	+			H	20.1	4.6	7.2	2.3	38.4	47.5	0.11	0.69	0.07	0.17	0.43	40	3	5.0	37
Machaerina angustifolia¯	L	+			+	H	20.2	5.8	8.6	3.1	40.0	42.5	0.10	0.70	0.08	0.12	0.68	75	58	2.5	33
Machaerina mariscoides¯	L	+			+	H	24.1	8.3	6.3	1.8	37.2	46.4	0.09	0.38	0.11	0.09	0.77	35	30	2.0	14

Oplismenus hirtellus†	L/s	+			+	H	10.8	13.9	18.0	2.4	17.9	47.8	0.24	3.63	0.99	0.88	0.06	360	76	9.0	47
Paspalum conjugatum‡	L	+	+	+	+	H	16.6	7.2	12.2	1.3	32.3	47.0	0.16	2.04	0.14	0.63	0.06	140	177	8.0	33
Peperomia sp.-	L/s	+			+	H	10.6	8.5	13.4	7.3	18.8	52.0	0.14	1.55	0.92	1.21	0.17	3208	206	8.5	105
Psidium cattleianum‡	F(pulp)	+	+	+		t	16.7	4.1	3.0	5.1	17.9	69.9	0.04	1.17	0.12	0.08	0.22	16	29	7.0	55
	F(seed)	+	+	+		t	25.5	1.4	5.4	8.3	60.8	24.1	0.11	0.14	0.34	0.06	0.03	9	22	10.5	65
Rubus hawaiiensis-	F	+				t	11.1	3.2	10.6	9.0	28.6	48.6	0.18	0.84	0.14	0.27	0.23	118	161	12.0	53
Rubus rosaefolius‡	F	+	+			H	12.6	3.5	8.8	15.3	30.3	42.1	0.12	1.06	0.08	0.19	0.04	59	71	9.0	50
Sadleria sp.-	r				+	H	20.2	4.0	4.3	0.8	25.1	65.8	0.08	0.45	0.16	0.34	0.41	52	1745	14.5	38
Scaevola chamissoniana-	L/b				+	t	11.7	10.6	15.5	7.8	17.6	48.5	0.14	2.27	0.66	0.74	1.13	367	77	10.0	100
Uncinia uncinata†	L	+			+	H	27.4	4.2	8.2	1.8	32.6	53.2	0.08	1.29	0.11	0.20	0.10	290	498	8.5	40
Vaccinium sp.-	F	+				t	12.5	2.7	8.4	10.9	16.3	61.7	0.14	0.67	0.24	0.10	0.05	169	49	9.5	103

Other plant foods not subjected to proximate analyses:

Deschampsia nubigena-	WP				+	H
Hypochaeris radicata‡	R	+			+	H
Marattia douglasii-	r/f				+	H
Metrosideros polymorpha-	L	+	+			t
Psychotria sp.-	b			+	+	t
Sacciolepis indica‡	L	+			+	H
Spathoglottis plicata‡	B				+	H

Key to notations:

* on dry matter basis
° Polynesian introduction
- endemic
‡ exotic
† indigenous
O stomach contents
● droppings
Δ direct observation
▲ feeding sites

H herb
T large tree
t tree
wv woody vine
DM dry matter
A ash
CP crude protein
EE ether extract
CF crude fiber
NFE nitrogen-free extract

S seedlings
F fruit
B bulb
R roots
yf young frond
L leaves
r rhizome
s stem

tc tree core
st stipe
f frond
Fl flower
C corm
b bark
WP whole plant
Sh shoots

Pigs fed in characteristic ways on different plant species. Young shoots, leaves, and fronds were selected over older parts. Freycinetia arborea were bitten at the crown; the apical stem was fed on from base towards the shoot apex, leaving the rosette of leaves at the feeding site. Lateral buds that arose after the growing apex had been fed on were eaten whole. Astelia plants were generally pulled rather than rooted off the ground and bases of tree trunks; bulbs and roots, but not leaves, were eaten. Root tubers of Hypochaeris radicata were obtained by digging, and eaten whole. Leaves and flowers were rejected and left at the feeding site. Pigs seemed to be able to root older plants in preference to younger ones.

Most low-growing herbaceous plants were eaten from the shoot downwards. Foot-high Broussaisia arguta were frequently seen with the shoots and young leaves nibbled away. Pigs raised their heads to reach for younger fronds of Athyrium. When feeding on Eupatorium, leaves were stripped off the plant and eaten in preference over the stems. Rooting was minimal when pigs forage on Hydrocotyle. Leaves were pulled and eaten; the long creeping stems were neither rooted for nor eaten. Rhizomatous parts of Marrattia douglasii were eaten whole, so were the younger fronds. Lobeliads (Trematolobelia sp.) were uprooted; roots, bark and young leaves served as food.

When feeding on grasses and sedges, leaves at the center of the plants were usually browsed. Sedges (Uncinia uncinata, Carex alligata) besides being a plant food for pigs in ohia forest, were also the most commonly used and principal nesting material.

Debarking habits differed depending on tree species. Upright Clermontia trees and those epiphytic on Cibotium, and fallen trees were usually stripped of their bark in one or two feeding sessions. Foraging on Clermontia trees was exhaustive; bark stripping proceeded from trunk to apex and left fewer teeth marks than debarking on other tree species. These feeding activites kill the trees. Twigs, leaves, flowers, and fruits were eaten, often leaving only a tree skeleton. Overhanging branches were frequently reached for and pulled down for food. Debarking of Coprosma, Gouldia hillebrandii, and G. terminalis was commonly done with one to three bites at a time so that trees were killed over a few months after repeated feeding and complete bark removal. In Psychotria, bark removal was commonly associated with trunk tusking. In Scaevola, only the bark and shoots of the young, erect non-branching growing stage were eaten. Bark, wood, and leaves of Cordyline terminalis were usually eaten over a few feeding sessions. Field observations indicated that debarking of Coprosma, Gouldia sp., and Psychotria appeared to be the foraging activities of individual animals, but tree bark feeding of Clermontia, Cordyline terminalis, and trunk feeding of Cibotium sp. were more common than that of group foraging activities.

Pigs obtained the starchy core from tree ferns by feeding directly on upright, ground-trailing and fallen trees. Both species, Cibotium chamissoi and C. splendens were eaten. Upright trees were felled by cross-biting the trunk at a point about 0.6m above the ground. With group feeding, more than one pig could work together to fell an upright tree fern but this was not verified from field observations. Upright tree ferns felled by pigs were always troughed from apex to the base for the starchy core. Upright trees were sometimes fed on in their upright position by vertical stem troughing (Fig. 18) to as high as could be reached by the animal. Although vertical trunk troughing foraging posture was never observed, it was apparent that pigs stood on their hind feet to feed up the trunk. Vertical trunk troughing was certainly the foraging activity of adult animals. Ground-trailing tree fern would have been more accessible to pigs but are uncommon in the Valley. Hence, upright trees were the principal food source. Old tree ferns have hollow trunks and no starch core near their bases. These trees were usually felled by winds. There was no field evidence to suggest tree pushing by pigs, but pigs weaken tree ferns and contribute to their fall by rooting around the bases of the trees. Trees isolated by rooting were common on the Koukouai trail from 700 to 830m, and along the escarpment trail from 1040 to 1220m. Fallen tree ferns were troughed from apex to base like those felled by pigs. Feeding on tree ferns was always very exhaustive. Larger tree ferns that were not completely fed on were revisited for subsequent feeding until the trunk was completely troughed. Core feeding was more exhaustive than feeding on stipes, fiddleheads, or fronds. Fronds from upright trees were sometimes pulled down (Fig. 19), stipes and lateral stems were foods. Frond-pulling appeared to be a foraging behavior shown by younger animals. This foraging habit, once initiated on a tree fern was usually progressive in that all fronds were eventually pulled down, and the core was finally fed on.

Figure 18: Vertical troughing of standing tree ferns (<u>Cibotium</u> sp.) by feral pigs in Kipahulu Valley. Core feeding kills these native trees. Pigs stand (a,c) to trough high up the trees; this tree fern feeding method is restricted to adult pigs. Note that there is no feeding on fronds, stipes or fiddleheads of tree fern in (b).

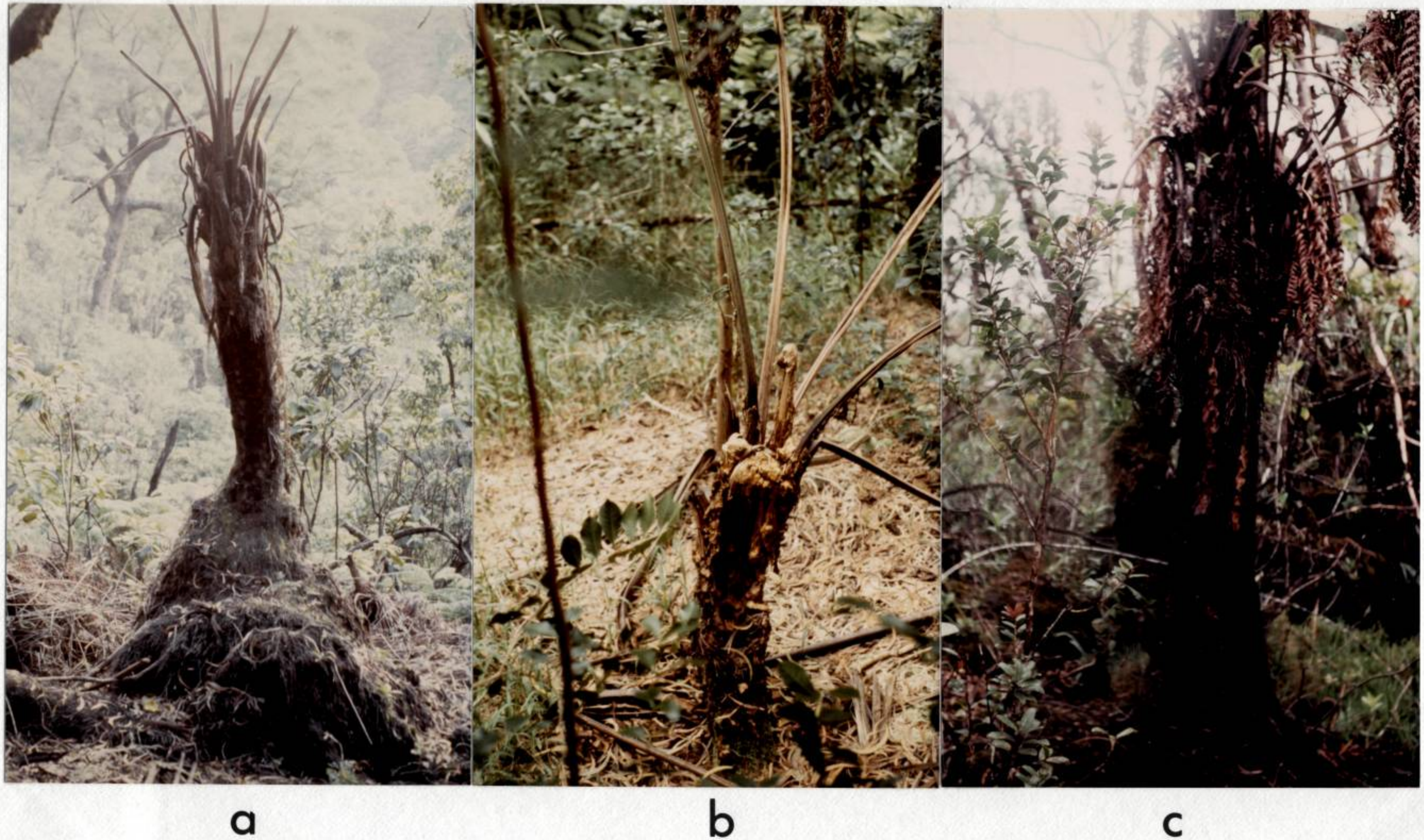

a
b
c

Figure 19: Tree fern (Cibotium sp.) frond pulling and feeding habits of feral pigs in Kipahulu Valley. (a) The early stages of frond pulling. Note the remains of the partially fed stipe on the ground, and the light trunk scarification. (b) Frond pulling often kills or deprives trees of live fronds. The lateral bud on the larger trunk has been eaten away. (c) Hollowed out trunk of a tree fern felled for food by a group of pigs. Note the pool of standing rain water in the hollowed out trunk which becomes a microhabitat for the breeding of mosquitoes.

a

c

b

Rooting was observed to be related to the search for earthworms. Rooting was shallow, seldom exceeded 20cm and may be explained by the vertical distribution of earthworms. All nine species of worms were litter and topsoil dwellers (Fig. 20a). Earthworm numbers varied with depth (Fig. 20b), with most of the worms occurring in the first 10cm of soil.

Rooting depth tended to increase in frequently rooted areas. In *Carex* bogs rooting was usually confined to litter and topsoil disturbance. Rooting depths in roseapple forest were generally deeper because of the abundance of earthworms and the greater depth to which *Pontoscolex corethurus* could be found (Table 13). Abundance estimates at three forest sites indicate highest density in roseapple forest soil and lowest density in ohia forest (Table 14). Earthworm density, however, was observed to be irregular at each site depending on drainage, soil type, pH, ground vegetation, presence or absence of organic matter, e.g. decaying logs, pig scats, and rooting frequency. In boggy areas, and ohia forest in general, earthworms occurred in the litter layer, roots of herbaceous vegetation and surface soil. Rooting depths in these areas were generally shallower than those at lower elevations. In boggy areas vegetated with *Oplismenus hirtellus* and *Paspalum conjugatum*, pigs spot or point-rooted for earthworms. Earthworms were swallowed whole; individual earthworms were identifiable to their taxon.

Figure 20: (a) Vertical distribution of earthworms in Kipahulu Valley. Horizontal line, vertical bar and line represent mean depth, standard deviations and range, respectively. Numerals indicate number of sampling sites.
(b) Depth distribution of earthworms in roseapple forest as determined by ten 0.5 x 0.5m quadrats.

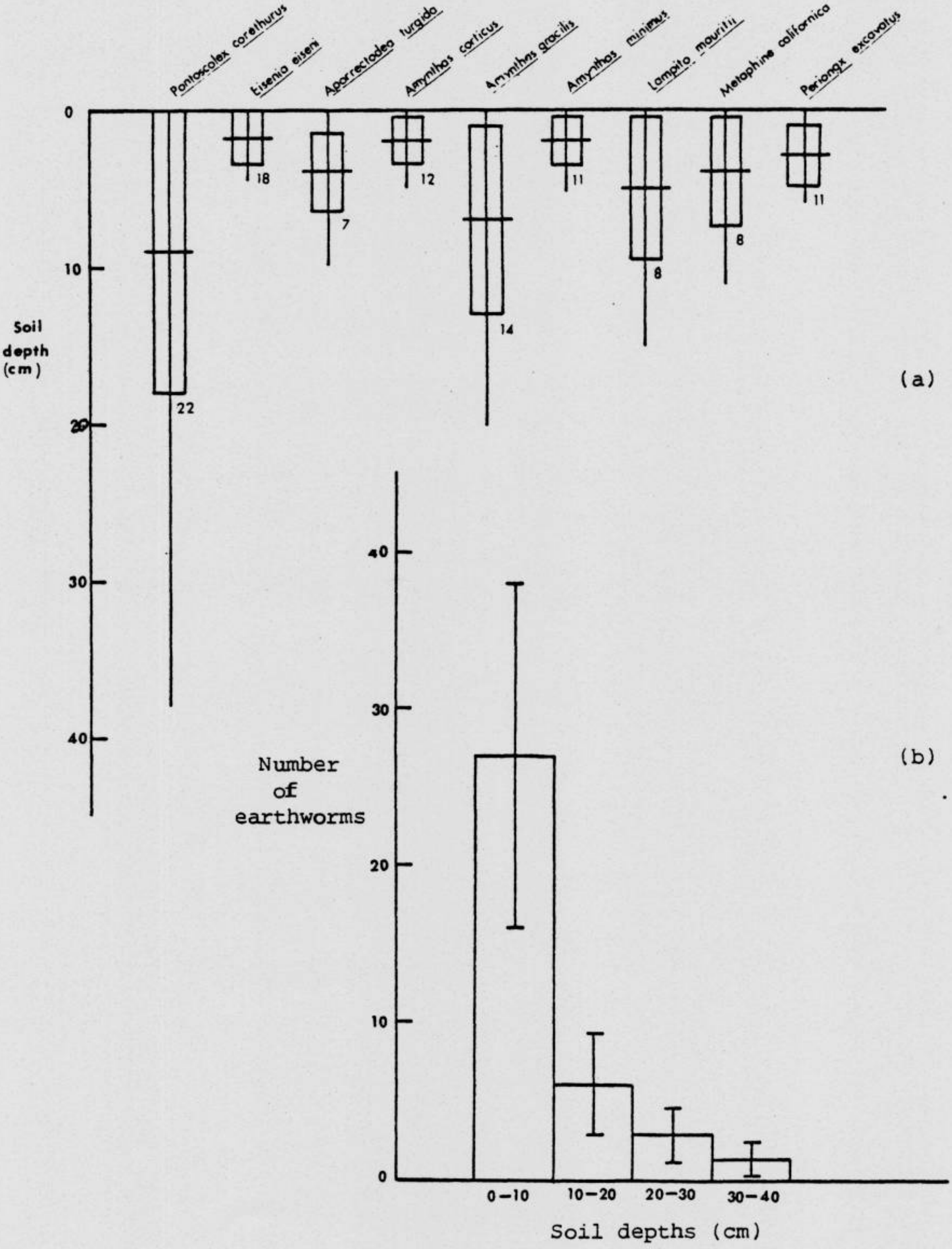

Pontoscolex corethurus
Eisenia eiseni
Aporrectodea turgida
Amynthas corticus
Amynthas gracilis
Amynthas minimus
Lampito mauritii
Metaphire californica
Perionyx excavatus
0
10
20
30
40
Soil depth (cm)
22
18
7
12
14
11
8
8
11
(a)
40
30
20
10
0
Number of earthworms
0–10
10–20
20–30
30–40
Soil depths (cm)
(b)

TABLE 13: Results of the analysis of variance for the effects of soil depth on the distribution of earthworms, in the roseapple forest, Kipahulu Valley. Analysis performed on 10 0.5 x 0.5 sampling units; soil depths stratified at 10cm apart.

Source of variation	SS	df	MS	F
Total	5623.8	39		
Soil depth	4246.9	3	1415.6	37.1[1]
Error	1376.9	36	38.2	

[1] P < 0.001

TABLE 14: Abundance of earthworms at three forest sites in Kipahulu Valley.

Sampling site	N[1]	Sampling depth (mean ± SD)	Numbers per m^2 (mean ± SD)
Roseapple forest, E600m	10	37.5 ± 6.1	146 ± 61.3
Koa forest, E920m	10	33.1 ± 9.3	69.2 ± 35.4
Ohia forest, E1450m	10	18.5 ± 12.3	31.6 ± 25.5

[1] Sampling units were 0.5 x 0.5m quadeats.

(g) Nutrient quality of plant foods

Most of the dry matter of plant foods was carbohydrate (Table 12). Nitrogen-free extract (NFE), i.e. sugars and carbohydrates, was relatively high, but protein, fat and mineral content were low. Twenty-five of 36 food items had total carbohydrate in excess of 75% dry matter. Tree fern core had the highest NFE (83.2%) among all plant foods, and low crude fiber (9.1%). Stipes of tree ferns were, however, twice as fibrous and considerably higher in crude fat. Sedges (Carex alligata, Uncinia uncinata, Machaerina sp., and Cyperus) ranked after tree fern in total carbohydrates (more than 80%), but CF made up the bulk (32-40%) of the DM. Other plant foods with NFE more than 70% were strawberry guava, roseapple fruit (Table 12), Colocasia esculenta, and bark of Cordyline terminalis. Nitrogen free extract in leaves of plant foods exceeded 40%; CF was relatively high.

Ether extract in the proximate analysis represents neutral fat and is generally taken to represent crude fat in the forage. Crude fat, with the exception of kukui nuts, varied from 0.3 to 15.3. This index was higher in dicotyledonous than monocotyledonous plant foods. Protein was not a major constituent in the plant foods. Foods with crude protein (CP) in excess of 20% were represented by the young fronds of Athyrium, Acacia koa seedlings, and fruits of Aleurites moluccana. Foods with CP more than 10% were leaves of Cheirodendron trigynum, Eupatorium, Hydrocotyl, Oplismenus hirtellus, Cordyline terminalis, bark of Coprosma, Scaevola, and Dicranopteris, and fruits of Rubus hawaiiensis. Strawberry guava (pulp) was a poor source of protein (3%

DM); CF and CP were, however, higher in the seeds, but these nutrients were not available to pigs. Tree fern was low in protein; CP (5.1%) in the core was higher than that in either stipes (2%) or strawberry guava. An inverse relationship between CP and CF was present in most plant foods.

Ash varied from 1.4 to 11.5% of dry matter. This fraction includes silica and other non-nutritional constituents. Inorganic residues represented by the ash fraction showed that minerals were very diluted in plant foods. Among fern foods, Athyrium had the highest nutritive index for K, P. Ca, Mg, Cu, and Zn. Mineral content was higher in grasses than sedges and ferns. Fern foods were poor sources of calcium and phosphorus. Calcium ranked the highest in two endemic plants, Freycinetia arborea and Broussaisia arguta. Dicotyledonous plant foods had higher mineral content than monocotyledonous foods.

Discussion

(a) Characteristics of food habits

Food habits of feral pigs were characterized by: (1) an omnivorous diet consisting largely of plant matter, (2) a staple diet of tree ferns, (3) a seasonal switch to strawberry guava when the fruit was available, and (4) a strong reliance on earthworms as a source of animal protein.

Omnivory in the feral pigs was evidenced by feeding at two trophic levels. Plant matter formed the bulk (more than 93%) of the diet and was largely derived from above the ground. Animal matter was subterranean in origin, although ground and arboreal invertebrates, which were of lesser importance, were also represented in the diets. Food habits of feral pigs (Springer 1977; Barrett 1978; Giffin 1978; Wood & Roark 1980) and the wild boar (Asahi 1975; Scott & Pelton 1975; Howe et al. 1981) in other habitats were similarly characterized by omnivorous diets composed largely (more than 90%) of plant matter.

Results from this and other studies (Baker 1975; Giffin 1978) show the diets of feral pigs in Hawaiian rainforests were comprised principally of tree ferns. Tree fern was the staple food for feral pigs in Kilauea forest on the island of Hawaii (Mueller-Dombois et al. 1981), Hawaii Volcanoes National Park (Baker 1975) and in the Kohala, Laupahoehoe and Upper Waiakea rainforest reserves on Hawaii (Giffin 1978). Above the upper limits of the tree fern distribution pigs fed on plants which are characteristic of seasonal alpine habitats: grasses, root tubers and fruits. Feral pigs in the alpine grassland on Kalapawili Ridge, Maui (Jacobi 1980) and those on the Mountain pasture habitat on Mauna Kea, Hawaii, had gosmore (Hypochaeris radicata) as their staple foods while those on Mountain scrub-forest on Mauna Kea, Hawaii, had ohelo (Vaccinium reticulatum) as their staple. Differences in dietary composition for pigs in rain forest, mountain scrub-forest and alpine grassland can provide clues on pig movements and dispersal patterns through stomach analyses.

Why is the tree fern eaten in preference to other plants? Three reasons are advanced to explain this food habit. Firstly, tree ferns are still an available and in some areas a locally abundant food source in closed rainforests (Zone D2 of Ripperton & Hosaka 1942) from 300-1800m. Secondly, tree fern core is a high energy food; the energy content is comprised essentially of sugars and starches that are highly digestible (see below). Proximate analysis show that no other plant foods in this study area approach tree ferns in energy content per unit weight (Table 12). Feral pigs exploit tree ferns primarily for their energy requirements; their strong preference for this food is, without doubt, due to the soluble sugars (sweetness). Thirdly, tree fern is selected as a staple food because of the large quantity (volume) of food it contains. As an example, a mature tree fern with a trunk height of three meters and a core diameter of 10cm will yield a core volume of $2.35 \times 10^2\ m^3$. Assuming a stomach volume 3.2 liters and a 24-hour stomach emptying, this food volume would fully feed a group of seven pigs or an adult pig for at least seven days. Thus, pigs could obtain a large quantity of several high energy meals from one felling of a tree fern.

Feral pigs readily switched from a tree fern diet to a diet of strawberry guava when the fruit was available in the fall. Diet shifts such as this have been reported by other workers. Giffin (1978) noted that feral pigs in rainforest habitats on Hawaii shifted from their tree fern diet to a diet of banana poka (*Passiflora mollissima* (HBK) Bailey) when the fruit was seasonally available. Barrett (1978) observed a sudden shift in the diets of feral pigs from wild oats (Avena barbata Pott. ex Link.) to acorns (Quercus) and manzanita berries (Arctostaphylos) as soon as each food became available. Similar food shifts have also been reported for feral pigs in Texas (Springer 1977) and South Carolina (Wood & Roark 1980). The pigs' ability to take advantage of seasonally available foods rather than seek out scarce out-of-season foods is an optimum foraging strategy in that energy intake is maximized while time spent in food searches is minimized. Some seasonal foods have higher nutritive value and continuous feeding on the season's foods would build fat reserves to help tide over any environmental food constraints in the following season.

Oligochaetes were the most important all-year source of animal food. Percentage occurrence and volume composition of earthworms in the diets of feral pigs were higher than those reported in other studies. The abundance of earthworms, their occurrence over a wide pH range (3.3-7.1), and their habits as surface or top soil dwellers accounted for the importance of this food item. Feral pigs indirectly assisted in providing nitrogenous foods to earthworms by their defecating and urinating on rooting plots. Although nine species of earthworms were found in the soils, Pontoscolex corethurus was more commonly represented in the ingesta than the other species, suggesting preferential feeding. Earthworms differ in palatability (Gates 1972; Easton 1979 London - pers. comm.). Preferential feeding on P. corethurus may be due to palatability and its larger size. Additionally P. corethurus contracts violently when uprooted and thus may be attractive to pigs more than the other species.

No vertebrate foods were found in the stomachs, except for fragments of pig bones in the stomach of one lactating sow. Pigs occasionally fed on pig skeletons. Calcium is lost by sows through milk, and bone feeding was perhaps one way of replenishing this mineral.

Lack of vertebrate foods in the pig's diet is not necessarily evidence that pigs do not interact with other vertebrate fauna in the Valley. Feral pigs are known to feed on the eggs and goslings of the ground-nesting Hawaiian goose (*Branta sandvicensis*) (Kier & Berger 1980) and suspected of preying on the Newell shearwater (*Puffinus puffinus*), the Hawaiian dark-rumped petrel (*Pterodroma phaeopygia*), the Hawaiian owl (*Asio flammeus*) and the Hawaiian duck (*Anas wyvilliana*) (Warshauer 1980). On Auckland Island, New Zealand, feral pigs are known to search the burrows of petrels for eggs and young birds and to feed on other sea birds. Other studies have shown that vertebrate foods could be as diverse as mole, frogs, birds (Asahi 1975); rodents, cattle, deer, fish, snakes (Springer 1977), animal carrion (Barrett 1971), salamander (Scott & Pelton 1975), sea lions (Challies 1975) and sheep (Hone & O'Grady 1979). Since vertebrates are more mobile and have better escape behavior, the pig's predation on vertebrates as food source are often directed at the eggs or young of the animals.

(b) Impacts on rain forest ecosystem

Food habits of feral pigs were particularly damaging to the structure and dynamics of the rain forest ecosystem. Feeding pressures were directed at no less than 40 plant foods, 75% of which were native plants in the herbaceous understory and subcanopy layer. Over 90% of the diets were obtained above the ground principally through tree-felling, debarking and cropping. This food habit contrasts with that for the boar in Great Smoky Mountains National Park (GSMNP), Tennessee, where 71% of the diet was subterranean in origin (Singer 1981). The most direct damage to the rainforest was the reduction in the abundance of native trees (e.g., _Cibotium chamissoi_, _C. splendens_, _Clermontia_, _Gouldia hillebrandii_). Continuous feeding pressure on these evergreen plants could potentially eliminate or reduce some populations. Local plant extinctions produced by the pigs' selective food habits have been observed in Tennessee (Bratton 1974). On Auckland Island, New Zealand, Challies (1975) reported that feral pigs virtually eliminated several species of endemic plants.

The most serious threat to the stability of the rainforest lies in the triad formed by the pig (exotic), tree fern (native), and strawberry guava (exotic). In this three-way interaction, both tree fern and strawberry guava served as staple foods for the pig. The damage to the rainforest may be discussed by examining each of these food chains: pig-tree fern, pig-strawberry guava, and the tree fern-strawberry guava interaction.

Pigs interacted with tree ferns at 3 levels: (1) direct predation, (2) disruption of regeneration, and (3) destruction of the sub-canopy layer. Foraging habits killed and reduced the abundance of tree ferns. The standing biomass was dominated by mature trees (Yoshinaga - unpubl. data). Ground-trailing trees are common in rainforest with light pig activity (Mueller-Dombois et al. 1981), but were uncommon in the Valley. Fallen trees usually continue to grow and frond upright by establishing a root system at a new base, but fallen trees were troughed out for food before they could reestablish themselves. Feeding pressure will probably increase when tree ferns are rare or when pig density is high. At low levels of abundance, tree ferns could still be eaten out at a faster rate because pigs could eat many alternate but less preferred foods. The carrying capacity of pigs may be dependent on tree ferns. Thus, the number of pigs which can be supported in the Valley or other forest may be determined by the density of tree ferns.

The year round felling of tree ferns of all size classes most probably affected the trees' regeneration. The switch in diet from tree fern to strawberry guava during early winter was of little consequence in the recovery of this tree primarily because of its very slow growth rate. Growth statistics (Cibotium chamissoi) on an annual basis were: 1.34kg of starch core, 5 fronds, vertical growth of less than 11cm and bole diameter increment of less than 0.3cm (Ripperton 1942). This very slow growth would mean that the trees were eaten out at a rate faster than they could be replaced. Hence, tree fern represents a diminished food source. The destabilizing factor in the ecosystem can be expected to increase as this food is progressively reduced by pigs. Feral pigs further affected tree fern regeneration by rooting activities. Rooting removed the liverwort and moss ground cover, thus depriving tree ferns of beds for spore germination.

The tree fern subcanopy was destroyed each time a tree was felled for food. Tree ferns provide a very special spatial dimension for many rainforest plants. Native trees (Cheirodendron trigynum, Clermontia) and Freycinetia arborea are often epiphytic on tree ferns and hence add considerably to the total subcanopy cover. Loss of tree fern biomass through direct trunk feeding, or basal rooting could bring about a substantial cover loss. Canopy loss has a destabilizing influence on native ecosystems. Light stratification to the forest floor is modified and this alters the composition of shade tolerant understory and ground vegetation in favor of exotic species. Ecosystem studies in the Hawaiian islands have demonstrated that tree ferns are the most important stabilizing factor in rain forest and that any man or animal induced tree fern removal will inevitably bring about a rapid invasion of exotics (Mueller-Dombois et al. 1981). Thus, the rapid increase in the exotic plant species pool in the Valley since pig occupation in 1945 could be linked, in part at least, to tree fern depredation.

The pig-strawberry guava food chain, unlike that in tree fern, did not end at feeding (Chapter 7). This exotic animal-exotic plant association had a spatial-temporal dimension in that the pig assisted in the dissemination of the strawberry guava throughout its range. In so doing the pig increased the distribution range of this plant food. The temporal dimension of this interaction was exemplified by the fact that the pig-aided dispersal accelerated the spread of this shade tolerant plant in new areas under the forest canopy. This weed is an active invader in rainforest (Mueller-Dombois et al. 1981) and damages native forest formations by successfully outcompeting native plants. Replacement of native forests by guava stands established by feral pigs has already been reported by Judd (1936). Thus, in the three-way interaction, the pig reduces tree ferns and the subcanopy cover, but increased the standing crop of strawberry guava. While one food resource was depleted by the food chain, the other food source was increased. It is through the latter food chain that feral pigs threaten to displace native forest with the exotic invader.

Presence of koa leaves and seedlings in stomachs suggest that feral pigs might be disruptive to the reproduction cycle of the native legume tree (<u>Acacia</u> <u>koa</u>). Pig-koa interaction was somewhat complex. Koa seedlings sprouted readily in pig-disturbed areas, and even on disturbed B-horizon soils, but were less frequently seen on rooted sites vegetated by exotic plants. Koa seedlings and leaves were not present in bulk, but the percentage frequency occurrence was relatively high (Table 12). Koa leaves had the highest crude protein among all plant foods and would be a good source of dietary protein for juvenile animals. Field observations showed that seedlings that sprouted on disturbed sites were foraged during subsequent rootings. Since it could be assumed that seedlings that were eaten would not normally have sprouted if the ground had not been disturbed, then seedling removal would not be of any importance in disrupting koa regeneration. However, Becker (1976) noted that the stability of rainforest may be disturbed through reduction in koa trees at high pig density. The present study seems to suggest that koa regeneration on rooted areas was inhibited by competition with faster growing exotics rather than by seedling removal. Exotic plants that carpet disturbed sites probably deprived koa seeds of light that is needed for germination.

Rooting removed ground vegetation from the forest floor and initiated localized top and sub-soil erosion and produced seed beds for exotic weed invasion. Surface rooting exposed topsoil to rainwash, while topsoil rooting loosened the soils and mixed litter with uprooted soil. Soil disturbance probably affected the rate of nutrient cycling, litter decomposition and soil invertebrate populations. Singer (1981) observed that boar rooting decreased soil mineral content, probably through increased leaching. Rooting sites were generally re-rooted by the same group of pigs. The abundance and size of earthworms appeared to decrease in frequently rooted sites. Pigs responded to decreases in earthworm densities by increasing their rooting depth and rooting area at a rooting site.

The severity of erosion at disturbed sites was dependent on rooting depth and the topographic features of the sites. Uprooted soils in basin-like depressions were rapidly levelled by rain and flooding. Along gentle slopes, top soil erosion involved movements of loose soils to adjacent areas, producing in some areas a terracing effect or sediment ponds. Rainfall was an aggravating factor in soil removal at disturbed sites. Re-rooting at eroded sites frequently stripped the site of the topsoil, leaving a rooting scar--the yellow, clayey B-horizon soil. Erosion was less important in boggy areas and on low-lying grassy flats on the lower floor. Here pigs spot-rooted rather than root areally by rolling over ground vegetation. Rooting cavities acted as sediment traps for loose soils. Erosion undoubtedly increased the sediment load in the streams, and might adversely affect the native stream biota (Kinzie & Ford 1977), reduced recreational quality at Oheo, and affect marine productivity and in-shore fishing by coastal Kipahulu residents.

Ground scarification promotes exotic weed establishment. The dramatic increase in exotic plants since pig invasion in 1945 cannot be coincidental. Exotic plants increased from 5 in 1945 to 22 in 1967, and to 55 in 1980 (Yoshinaga 1980). This more than three-fold increase was represented largely by grasses (from 3 in 1967 to 14 in 1980), composites (from 4 in 1967 to 8 in 1980) and sedges (from 1 in 1967 to 8 in 1980). Increased pig activity and ground disturbance were the most probable reasons for the increase in exotic species pool. On pig-disturbed sites in the koa forest, the native herbaceous cover had been removed or reduced and replaced with exotic weeds (*Ageratum conyzoides* L., *Cyperus brevifolius* (Rottb.) Hassk., *Eleocharis obtusa* (Willd.) Schult., *Sacciolepis indica* (L.) Chase, *Eupatorium*, and *Eleocharis valvis*) (Yoshinaga 1980). Boggy openings previously vegetated by the native sedge, *Carex alligata*, had been replaced with invasive exotics, Paspalum conjugatum Berg. or Cyperus haspan L.; the latter species was an early colonizer of pig-disturbed sites.

The replacement of forest formations by grassy or weedy formations through progressive pig activities are well known. This process seems to progress at a faster rate in rainforest probably because high rainfall favors faster growth in weedy exotics. Similar patterns of vegetational changes have been reported from other areas. Feral pig activity in alpine habitats reduced the cover of an endemic grass, Deschampsia australis Nees ex Steud., to one dominated by an exotic grass, Holcus lanatus L. (Mueller-Dombois 1967; Jacobi 1980). Reduction in herbaceous cover and changes in herb community structure due to boar activites in GSMNP had been documented by Bratton (1974, 1975).

Feral pigs had been suspected to contribute to the extinction or decline of native forest birds via the mosquito-avian malaria cycle (Warner 1968; Baker 1975). Wallows and, in particular, troughed tree fern trunks were believed to provide microhabitats for the breeding of Culex pipiens, a vector of avian malaria. Warshauer (1980) stated that breeding habitats for mosquitoes in Hawaii Volcanoes National Park were produced exclusively by feral pigs. This statement seems incorrect because in the Valley's rainforest, standing water for mosquito breeding exists in tree cavities, trunk axils, forest floor and at bases of fallen trees. It seems very unlikely that the distribution of mosquitoes was limited by the number of naturally occurring breeding sites in the rainforest. Pig activities, however, did contribute to an increase in the number of breeding sites. Tree ferns that were felled for food were initially hollowed by pigs and later by rats or gradual decay. Troughed out trunks also provided cavities for standing water. Larvae of Culex mosquitoes have been observed in pools of standing water on pig-abandoned tree fern trunks and were more frequently used than wallows as breeding sites.

Differences in food habits between pigs in this habitat and populations in other habitats are apparent from this study. Plant foods are derived principally from above the ground. This food habit contrasts with that for wild populations in Tennessee and most feral populations on the mainland where the bulk of the plant matter was subterranean in origin. Staple foods available in rainforest are exceptionally good sources of energy, and are superior in energy content to acorns and most other major foods for pigs in other habitats. Earthworms are the most important source of protein, and probably calcium; the importance value of this dietary protein for pigs in the rainforest was higher than for pigs in other free-ranging populations. Studies of food habits indicate that feral pigs were very unlikely to be energy or protein limited. Blood biochemical values support the tentative conclusion of adequate nitrogen intake (Chapter 10), and further show that the protein status of feral pigs were comparable to normally fed domestic pigs and superior than free-ranging populations in some habitats.

The impact of the pigs on the rainforest is probably more severe than pig damage in continental habitats because of differences in evolutionary history and the greater sensitivity of insular environments to habitat perturbations. Feeding activities are directed at the same species populations throughout the year. This is unlike pigs in seasonal habitats where feeding activities follow the available plants of the season. Most unique and perhaps ecologically devastating to native forest stability is the pigs' food preference for tree ferns and destruction of the subcanopy stratum occupied by tree ferns. But all aspects of the food habits are damaging to the native forest. Rooting initiates soil erosion; producing seed beds, and promotes invasion of exotic weeds; and removes moss, liverwort, and native herbaceous ground covers which are replaced by non-native species. Direct feeding on native trees reduces their abundance and affects tree regeneration. Finally, the feral pig assists the strawberry guava to replace native forest formations through the open food chain it forms with this active tree invader.

CHAPTER 7

DISPERSAL ECOLOGY OF THE STRAWBERRY GUAVA

Introduction

Seed dispersal is the active process of transporting seeds away from their sites of production. When animals are agents of seed dispersal, seeds may be transported by, on or in the animal (Pijl 1968). Anecdotal accounts of these dispersal methods have been well documented (Ridley 1930). Earthworms (Ridley 1930), birds (Smythe 1970), ungulates (Burtt 1929; Lamprey 1967; Lamprey et al. 1974) including wild pigs (Phillips 1926) and feral pigs (Mueller-Dombois et al. 1981) are known to actively disperse many seed plants via gut transport of ingested seeds. Only recently has seed dispersal ecology been recognized as pertinent to the understanding of community interactions (Bullock & Primack 1977).

The strawberry guava, Psidium cattleianum, is an agressive invader (Mueller-Dombois et al. 1981) and noxious woody weed (see Literature Review) in Hawaiian ecosystems. Feral pigs, goats, sheep and cattle have long been recognized as important dispersal agents of this species (MacCaughey 1917). In Kipahulu Valley, P. cattleianum presently occurs in montane rain forest from sea level to 1170m (Yoshinaga 1980). Under the present conditions, native plants cannot compete successfully with this aggressive weed which excludes all other indigenous plants by forming densely shaded monospecific stands broken only by gulches and forests of rose apple (Eugenia jambos). Feral pigs were thought to be the primary agent for disrupting the native ecosystem and aiding the spread of strawberry guava and other introduced plants (Lamoureux & Stemmermann 1976) by transporting seeds in their gut. An understanding of the effects of gut transport on seeds of P. cattleianum is needed for assessing this role of the feral pig in the dispersal of the plant.

The purpose of this study was to investigate the importance of the pig as an agent in dispersal and germination of the strawberry guava. Effects of endozoochory on the guava seeds were included in the study. Specific questions raised at the outset of the study were: (i) How are the seeds transported? (ii) How does passage of seeds through the digestive tract of the pig affect seed structure, viability and germination? (iii) Are seeds effectively transported in the gut? and (iv) What are the ecological and management implications of this pig-aided dispersal?

Literature Review

(a) Historical background

Psidium cattleianum Sabine belongs to the family Myrtaceae. Indigenous to Brazil, the geographic range of the species extends from Rio de Janeiro, Minas Gerais, to Uruguay (Correa 1926). Known as araca da praia, araca-vermelho and araca-do-campo in its native home (Popenoe 1934), the species had been carried as an ornamental plant and for its fruit to all tropical and subtropical regions of the world (Merrill 1954).

Portuguese explorers were presumed to have introduced the plant into Southern China (Popenoe 1934). During the botanical explorations of eastern Asia by European travellers in the 1800s, two Englishmen, Barr and Brookes, in 1818, brought seeds of the strawberry guava and other Chinese plants into Europe (Bretschneider 1898). For some years the species was erroneously thought to be a native of China and became known by such names as the Chinese guava, Psidium chinensis and Psidium sinense. It was not until 1824 when Lindley pointed out the mistaken belief and traced its origin to the New World (Lindley 1824).

In 1820, William Cattley became the first to succeed in cultivating the strawberry guava. He obtained two crops of fruits from the plants he grew with the seeds he bought from Barr and Brookes. Cattley found that the plant could be propagated by cuttings. In the same year, he described the species of Psidium in a letter to Sabine, the Secretary of the Royal Horicultural Society, London, as having "Coriaceous obovate leaves...fruits which are spherical, deep claret colour and growing in the axillae of the leaves" (Cattley 1821, see also Fosberg 1941, Corner 1976, for further botanical description of the species).

Sabine, in 1821, named the plant P. cattleianum, after William Cattley for the latter's botanical species description. He further described the fruit and plant in Cattley's Conservatory (Bot. Reg. 8. 1822, F 622). Known commonly as the Cattley guava, original drawings of the species were made in 1821 by Hooker (see Notes by Secretary, in Cattley 1821) and Lindley (Bretschneider 1898). As pointed out by Fosberg (1941), the species name cattleianum, as accorded by Sabine to

Cattley in 1821, is often misspelled as cattleyanum. There may be another reason for this discrepancy. Historical records by Bretschneider (1898) revealed that Lindley was Cattley's first patron who drew, described and published many of Cattley's plants in Icones Braamianae and the Collectanea Botanica. Cattley, who financed both these publications may have been accorded the species name cattleyanum by Lindley. Although cattleyanum was used in older literature, its usage is increasing in more recent publications, for instance, Hillebrand (1965) and Corner (1976).

(b) Synonyms and varieties

A comprehensive review on the varieties and synonyms of P. cattleianum and P. littoralis has been given by Fosberg (1941). Some authors consider P. cattleianum and P. littoralis synonyms of P. variabilis (Popenoe 1934), but the latter two species have been included under P. cattleianum. P. littoralis has been used in preference to P. cattleianum by some workers, because P. littoralis was apparently the earlier specific epithet (Merril & Perry 1938). Differences in citation dates from title-page at the time an article was written and at the time it was published appears to be the cause of this discrepancy.

Two varieties of the strawberry guava grow wild in the Hawaiian Archipelago. More common is P. cattleianum which has reddish-purple fruits and is locally known as red waiawi or yellow cattley, waiawi-ulu'ula (St. John 1973), purple, or red guava. The other variety, P. cattleianum f. lucidum, also known as waiawi or yellow cattley guava, has larger sulphur yellow fruits. The common name cattley guava includes both varieties.

(c) Introduction into Hawaiian Islands

Like many other pantropic weeds, guavas were not present in Polynesia proper at first European contact (Merrill 1954). The common guava, P. guajava, was introduced into the islands in the early 1800s by the sea-faring Spanish botanist, Don Francisco Marin (Shiguera & Bullock 1976). Live plants of both varieties of strawberry guava were probably introduced into the islands from England on board the "Blonde" in 1825 (Degener 1932). Shortly after their introduction, both species became wild. P. guajava was reported to be growing wild in 1850 (Thompson 1941) and P. cattleianum was wild by early 1900 (MacCaughey 1917). Introduced birds and feral mammals were thought to be responsible for the rapid spread of the plants. Today both varieties of P. cattleianum grow together often in wet forests of the Hawaiian Archipelago.

(d) Economic importance and other uses

Psidium cattleianum is the most widely cultivated guava species in Central South America (Pio-Correa 1926) and the West Indies (Adams 1972). Except for cultivation in Fiji and Florida, the plant occurs semi-wild or wild elsewhere in its distribution. It has no commercial importance in Hawaii. Experiments in which fruits were subjected to near freezing temperatures showed that the fruit shrivel, ferment and decay very rapidly (Wilcox & Hunn 1914). Fruits are eaten, made into jams, gelatine, drinks, and, according to one Hana source, is good for making into wine.

Native uses of the common guava are well recorded (MacCaughey 1917, Ruehle 1948), as are its medicinal uses (Kaaiakamanu 1922). Less is known about the native Hawaiian uses of the strawberry guava. In South America, bark and leaves of the plant are used to treat intestinal problems; bark is also used for tanning and the stem as wood (Pio-Correa 1926). According to a local resident, Greig Lind, remains of cement pits, which were used by early Chinese immigrants for producing charcoal from both guava species, can still be located in the mountains of Hana, Maui.

(e) Weed characteristics

Occurring wild and under intensive cultivation, the strawberry guava is not a weed problem in Brazil (Oliveira 1980 Rio de Janeiro, Brazil - pers. comm.). Outside its native range, the species has been regarded as an aggressive weed or pest. In Hawaii and Fiji, P. cattleianum is classified as a noxious weed. In New Zealand, it is recognized as a potentially dangerous noxious weed. The following are some of the weedy characteristics.

(i) High tolerance for variation in physical environment.--Psidium cattleianum is found in tropical and subtropical parts of the world and in high montane environments. Its range includes India, Sri Lanka, France, Spain, Algeria and other Mediterranean regions (Popenoe 1934), Fiji, Jamaaica, Indo-Malesian region, the Philippines, Hawaii and other

Pacific islands, Florida, California and Cuba. It has an altitudinal range extending higher than 1220m (Popenoe 1934). The species withstands temperatures to -5°C and is grown for its fruits in localities too cold for other guava species (Ochse et al. 1961). It is fairly drought-resistant; withstands severe frost without injury; and succeeds in a wide variety of sites including rocky ground, red clay, sandy loam and wet forest soils.

(ii) High fecundity.—Large numbers of fruits are produced during the fruiting season. Seeds have high germinative power (over 90%) and possess a hard seed-coat, well adapted for short and long-range dispersal by birds and mammals. Seedlings are shade tolerant and grow well under parent plants. The plant reproduces readily from cuttings; cut stems sprout easily. Stem sections used for building corral traps grew regardless of whether the basal or apical end was planted in the ground.

(iii) Competitive ability.—The species forms very dense, continuous stands and excludes other shrubs or trees (Hillebrand 1965) presumably by limiting available light, nutrients and space.

(iv) Well developed insect and pest resistance.--Authors writing on guava pests do not differentiate between the common guava or the strawberry guava. It is, therefore, not possible to list pests specific to the latter species. However, it is well-known that, like the common guava, the strawberry guava suffers much less from attacks by phytophagus insects. In its native home, the plant is attacked by

Aleurodes cokerillae, Pyrrhopige charybdis and Stenoma albella (Pio-Correa 1926).

Materials and Methods

Coats of captured pigs were combed as part of the process of examining their role in transporting seeds on their exteriors. Seed materials and debris thus collected were sown in vermiculite at a fenced germination, site GS1 (640m), GS2 (910m) or GS3 (1450m), closest to the place of capture. In order to ascertain what seeds were carried by pigs in fecal matter, a total of 123 fresh droppings without obvious signs of strawberry guava seeds were collected and planted in vermiculite. Germination trays at each site were roofed over with white, transparent plastic sheets in which small holes were punched.

Fecal samples were examined in the field and laboratory for seeds. Seeds were extracted from each sample by washing through two soil sieves, were air-dried, and later counts were made of broken and unbroken seeds. Seed fragments derived from manually cracked individual whole seeds were found to occupy an approximate area of $9mm^2$. The number of seeds broken during mastication were estimated by spreading seed fragments of a fecal sample in a single layer on a grid and using the number of filled 3 x 3mm squares as an estimate of the number of broken seeds. One hundred whole seeds were randomly subsampled from each fecal sample and methodically examined under a dissecting microscope. Degrees of seed-coat scarification were identified and their frequency of occurrence recorded. Seed-coat and micropylar scarification were also studied under a scanning electron microscope.

Seed viability is generally tested by direct observation of embryos, X-ray analysis, tetrazolium staining or germination tests (Colbry et al. 1961, Hartman & Kester 1975). A germination test was used to investigate the effects of digestion on seed viability. The germination test was replicated six times; the first two replicates each consisted of 500 gut-treated and 200 untreated (control) seeds. The four other replicates each consisted of 100 of each type of seeds. Seeds from the same dropping were used for each replicate. Untreated seeds were extracted by hand from mature fruits collected randomly from the ground. Seed count, cross diameters and polar diameters were measured for each fruit. Seeds were germinated in vermiculite in a greenhouse and counts were taken daily as germination proceeded. Plumule emergence was used as the criterion for germination. Six replicates of 100 gut-treated and untreated seeds were germinated in vermiculite at GS1 and GS3. The latter site was in a guava-free area.

Results

(a) Description of the strawberry guava fruit

Flowering began from April to July and was profuse. Fruit-fall in trees from 370-670m on the upper plateau was from late August to December. Fruit maturity on any one tree or among trees was not uniform. Dropped fruits fermented and decayed within a few days, producing a strong aroma which carried quite a distance. During the duration of the study, fruiting was not observed on trees from 900-1200m; the latter elevation represents the present invasion front of the species, and the trees appear to be in younger age classes.

-3950ft el.

Proximate analyses (Chapter 6, Table 12) showed that the fruit was a poor source of calcium, phosphorus and magnesium. Dry matter, crude protein, crude fat, crude fibre, phosphorus, calcium, copper and zinc were higher in seeds than in the flesh; the fleshy part was high in nitrogenn-free extract (soluble carbohydrates). The higher nutrient and mineral contents in seeds were, however, not available to the pigs (see below).

Seed count per fruit ranged from 1-30 and the average number of seeds per fruit for 55 fruits randomly collected from the ground was 15.4. Cross and polar diameters for the smallest and largest mature fruits were 0.94cm, 0.98cm, and 2.83 and 2.64cm respectively. Correlation of seed number on cross diameter ($r=0.78$, $df=48$, $P<0.001$) were statistically significant (Fig. 21). Regression equations intersect at I (CD=PD); larger fruits were, hence, broader than longer (CD>PD) while smaller fruits were oblong (CD<PD).

(b) Species of seeds germinating from coats and from droppings

Plantings of materials collected from the coats of 18 animals yielded six seedlings from four samples; the species represented were *Carex alligata*, *Paspalum conjugatum* and an unidentified grass and sedge. In 123 plantings of fecal materials from August 1979 to September 1980 at the three germination sites, 18 contained seedlings (Table 15).

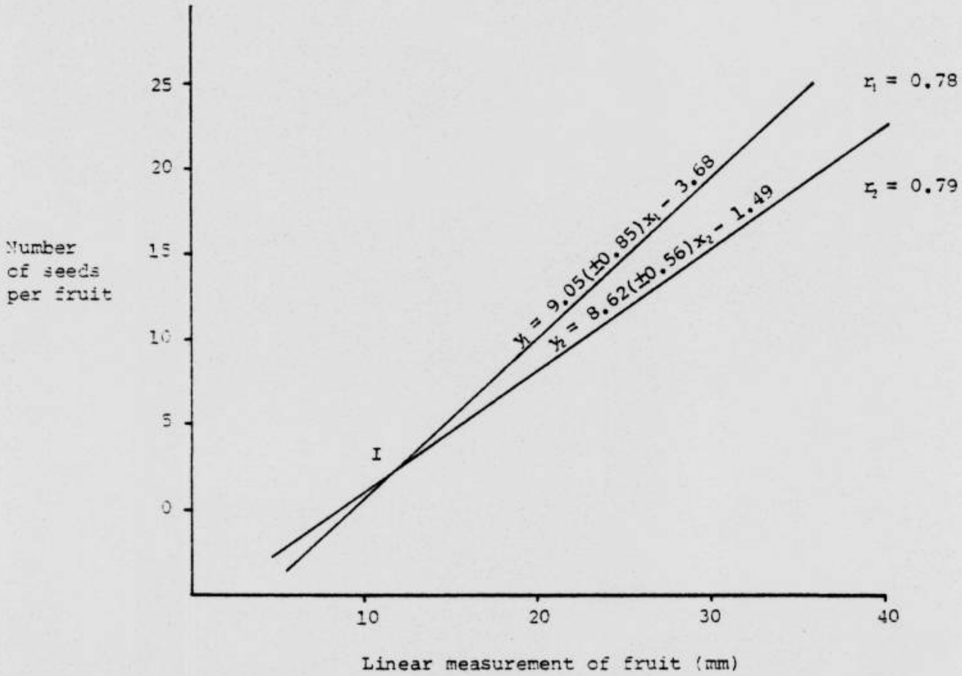


Figure 21 : Regression equations for seed count (y) per strawberry guava (*P. cattleianum*) fruit against the fruit's cross diameter (x_1) and polar diameter (x_2). Sample sizes for y_1 on x_1 and y_2 on x_2 were 50 and 55 fruits respectively.

TABLE 15: Seedlings recovered from 123 plantings of feral pig droppings from August 1979 to September 1980 in Kipahulu Valley.

Fecal planting sites	Number of fecal plantings	Number of plantings with seedlings	Species[1] of seedlings			
			PC	Pc	Rr	Unknowns
GS1	58	10	10[2](42)[3]	2(4)	2(2)	3(2)
GS2	36	6	6(6)	1(2)		
GS3	25	2			2(3)	1(1)
Total	123	18	16(48)	3(6)	4(5)	4(3)

[1] PC = *Psidium cattleianum*, Pc = *Paspalum conjugatum*,
Rr = *Rubus rosaefolius*.

[2] Number of fecal plantings containing seedlings.

[3] Total number of seedlings.

Psidium cattleianum was observed in 16 plantings, Rubus rosaefolius in four and P. conjugatum in three fecal plantings. Fecal plantings that were positive for P. cattleianum seedlings were grossly underrepresented, because droppings visibly loaded with guava seeds were not collected for planting.

The low number of species of seedlings recovered from droppings was contrary to expectations, but was supported by field observations. In situ germination of seeds of other species in pig droppings was observed only once for Paspalum conjugatum and twice for Rubus rosaefolius during the entire study period. Seedlings sprouting from fecal material were almost always that of P. cattleianum. Observations of high seed loads of P. cattleianum in pig droppings and in situ germination demonstrated pig-assisted dispersal and the establishment of P. cattleianum in large numbers on a new site. Germinants from three such pig droppings were separated and counted. The seedling counts were 762 ($600cm^2$), 250 ($400cm^2$) and 150 ($169cm^2$); the numbers in parentheses indicate the settled surface area of the fecal material at the time of the count.

(c) Fecal seed load

Over 90% of all pig droppings collected (N=48) or examined in the field (N=42) on the upper plateau from 600-850m contained seeds of the strawberry guava. These observations were made from September to December 1978, during an unusually rainy season. In most cases, droppings consisted of dense aggregations of guava seed, fruit coats, calyxes, and were typically loose, probably because of the high energy, low fibre diet. Droppings containing strawberry guava seeds were a useful indicator of the pattern of movement of pigs. Pigs feeding on the fruit at lower elevations often moved upslope into areas where the trees were not yet in fruit. Droppings containing guava seeds were observed up to 850m, but fruiting was observed only on trees below 700m.

Scat analysis showed that strawberry guava was the principal component of the pigs' diet during the guava fruiting period. Counts of voided seeds showed that an excrement of an adult animal could contain over 6000 seeds. Fecal seed counts in 19 adult droppings averaged 2875 ± 1037 seeds; this would correspond to an average of at least 187 fruits, assuming that fruit intake was proportional to fecal production. Less than 4% of the ingested seeds was found to be macerated by the teeth or later digestive processes. Therefore, the pig carries large quantities of physically undamaged seeds.

(d) Effect of gut treatment on seed germination

The final germination percentage was high in both gut-treated and untreated (control) seeds (Table 16); the difference in germination percentages was not statistically different. Therefore, the passage of strawberry guava seeds through the digestive tract of the pig did not affect the seeds' viability.

However, seed passage through the pig's gut resulted in earlier germination, as shown by the shift in germination curve towards the left (Fig. 22). This shift was brought about by two factors: (i) a reduction in the number of days to first germination, which was 16 days

TABLE 16: Germination parameters for gut-treated and untreated (control) seeds of the strawberry guava, *P. cattleianum* Sabine.†

Replicates	Number of Seeds		Final Germination Percentage		Germination Rate*		Germination Value**	
	Gut-treated	Untreated (Control	Gut-treated Seeds	Untreated Seeds	Gut-treated Seeds	Untreated Seeds	Gut-treated Seeds	Untreated Seeds
1	500	200	91.6	89.5	20.6	31.1	8.25	4.40
2	500	200	89.2	90.0	21.4	32.2	6.59	4.12
3	100	100	92.0	92.0	21.2	33.6	7.54	4.13
4	100	100	92.0	90.0	20.9	32.2	8.34	4.21
5	100	100	91.0	91.0	21.2	32.6	8.09	4.14
6	100	100	91.0	91.0	21.2	34.1	8.70	4.14

† Seeds for replicates 1 and 2 were derived from one pig dropping; those in replicates 3 to 6 were from another dropping. There was no difference in the final germination percentage between gut-treated and untreated seeds ($F = 0.97$, $P > 0.50$) but differences in germination rate ($F = 125.2$, $P > 0.001$) and germination value ($F = 144.1$, $P < 0.001$) were statistically significant.

* Mean number of days to 50% germination.

** Product of mean daily germination and maximum cumulative germination percentage during test. Index expresses the speed and completeness of germination.

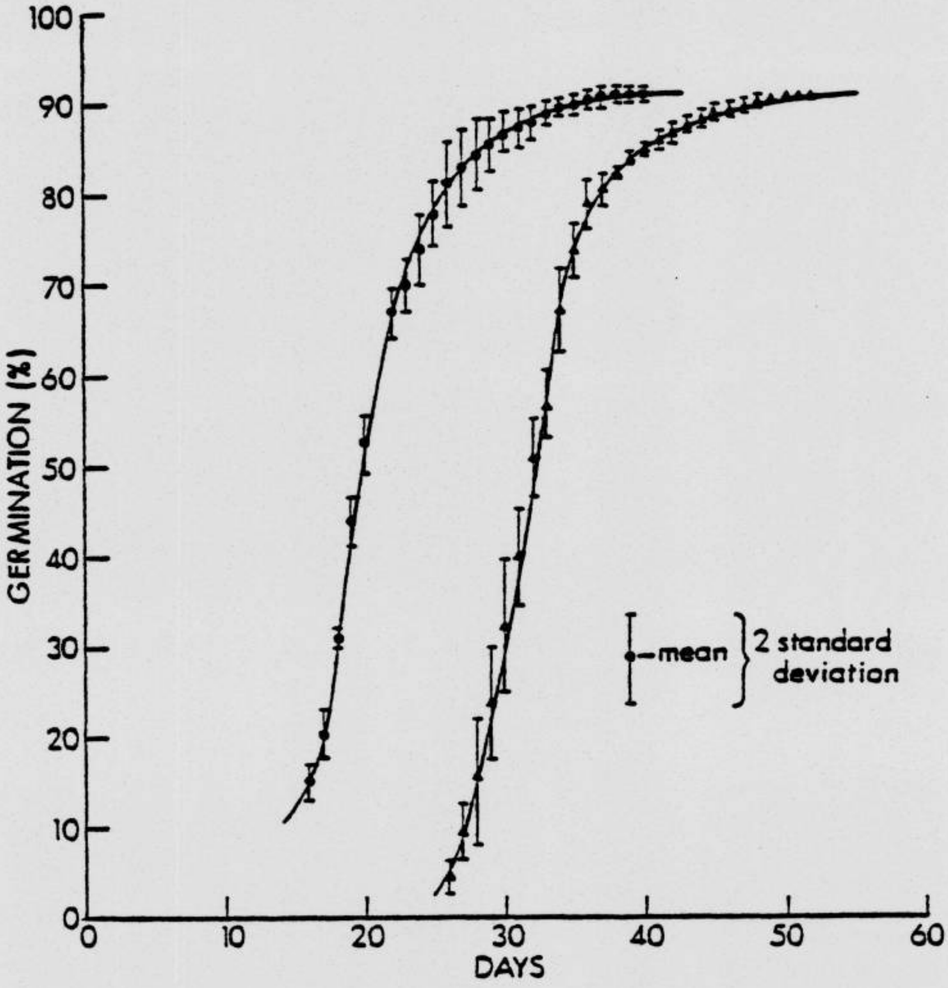


Figure 22: Germination curves for gut-treated (voided) and untreated (control) seeds of the strawberry guava, *Psidium cattleianum*. Daily means and S.D. are calculated from six germination trials in Table 16. ● voided seeds; ▲ control.

for gut-treated seeds as opposed to 26 days for the untreated (control) seeds; and (ii) the reduction in the time to 50% germination. The mean number of days to reach 50% germination, measured by the germination rate, was 21 days for digested seeds and 32.6 days for undigested seeds; the difference in germination rate was significant. The mean germination value which combines both the completeness and speed of germination was 7.92 for gut-treated seeds and 4.15 for untreated seeds; this difference was significant ($P<0.001$). Hence, gut-treated seeds germinate earlier and reach 50% germination faster than untreated seeds.

Germination trials for gut-treated and untreated seeds in the strawberry guava zone (GS1) and guava-free zone (GS3) in ohia forest yielded consistently high final germination percentages (Table 17). A two-way factorial ANOVA (Table 18) shows a significant difference ($P<0.001$) in germination rates between gut-treated and untreated seeds. The effects of sites on germination rates was also significant ($P<0.001$), but the effects of site on germination rates was not dependent on gut-treatment ($P>0.25$). Thus, strawberry guava seeds in the presently guava-free ohia forest could reach the same high final germination percentage recorded at lower elevations, and the number of days to 50% germination was increased at higher elevations.

(e) Effects of gut treatment on seed coat

During embryonic development, the ovule becomes inverted on its base, resulting in an anatropous condition, with the hilum lying close to the micropyle and the antiraphe more developed than the raphe (Corner

TABLE 17: Results of germination trials for gut-treated and untreated seeds of P. cattleianum in Kipahulu Valley.

Replicate[1]	GS1†(640m)				GS3‡(1450m)			
	Germination percentage		Germination rate[2]		Germination percentage		Germination rate	
	Gut-treated	Untreated	Gut-treated	Untreated	Gut-treated	Untreated	Gut-treated	Untreated
1	92	90	16	32	86	90	26	38
2	93	89	20	30	92	86	32	42
3	88	94	22	35	88	90	26	42
4	92	88	24	29	90	94	26	34
5	91	92	18	30	89	90	30	34
6	89	93	19	30	93	91	26	42
Average	90.8	91	19.8	31	89.6	90.1	27.6	38.6

[1] Replicates consisted of 100 each of gut-treated and untreated seeds. Gut-treated seeds in each replicate were derived from a different fecal sample.

[2] Mean number of days to 50% germination.

† Germination site within strawberry guava distribution range.

‡ Germination site above upper distribution range of strawberry guava.

TABLE 18: Summary table for a two-way factoral analysis of variance (ANOVA) on the effects of germination site (guava zone vs guava-free zone) and gut treatment on the germination rates of seeds of *P. cattleianum*.

Source of variation	SS	df	MS	F
Total	1274.96	23		
Cells	1097.46	3		
Germination site	360.37	1	360.37	40.62
Gut treatment	737.04	1	737.04	83.09
Germination site x gut treatment	0.044	1	0.044	0.0049
Error	177.50	20	8.87	

$P < 0.001$

$P > 0.25$

1976). Consequently, the embryo is curved. The seed is surrounded by a thick testa of highly lignified sclereids which form a very hard seed coat. However, the endotesta tissues around the micropyle are thin-walled and not heavily lignified forming the micropylar (sclerotic) plug through the seed coat. The position of the plug is very evident in the mature seeds because of a distinct cone-shaped protuberance in the center of which is the micropyle (Fig. 23a).

Some differences in seed-coat appearance and structure were observed in gut-treated and untreated seeds. Gut-treated seeds became greyish black, rough and dull. The discoloration was more intense around the hilum and micropylar areas. Scarification of the hard seed-coat, as observed under the dissecting microscope, was only superficial. Scanning electron micrographs showed some erosion of the macrosclereid cells in the seed-coat revealing the deeper layers of the multilayered sclerotic testa. Untreated seeds averaged 4.6mm (N=50) in length, whereas gut-treated seeds were 3.8mm (N=50) long. The difference in weight was untreated seeds 20µg, gut-treated seeds 18µg average weight.

Four types of seed-coat scarification were identified for all gut-treated seeds (Table 19). In Type I scarification, the anterior part of the micropylar plug and its rim remained intact (Fig. 23b). The sclerotic layer below the rim of the plug was eroded away, producing a cavity which may be continuous with the hilum. This was the most common and severe seed-coat scarification and occurred in 85.9% of all gut-treated seeds. In Type II scarification, the endotesta around the

Figure 23:Types of seed-coat scarification in seeds of the strawberry guava (*Psidium cattleianum*) after their passage through the digestive tracts of the feral pig.

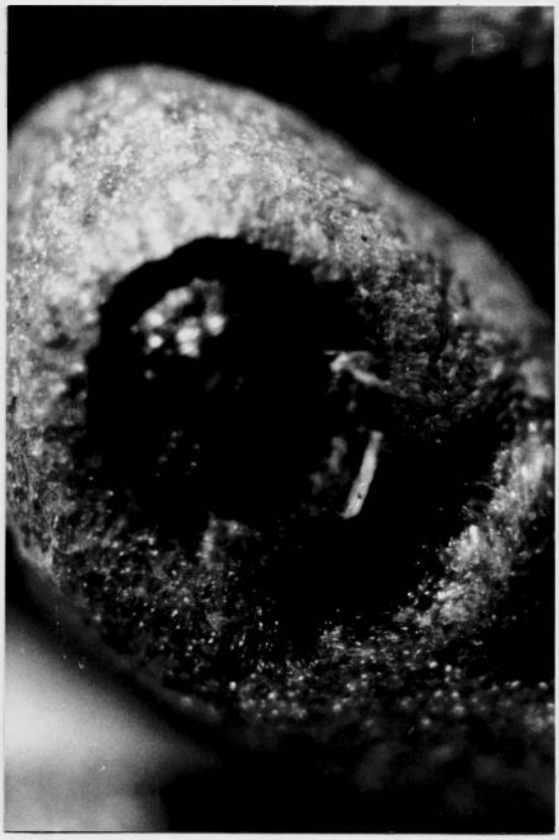
(a) Uningested seed. Note the very prominent micropylar plug, the micropyle, the close proximity of the hilum to the micropyle, and the vascular strand.

(b) Type I scarification. The anterior region of the plug and its rim are intact, but the sclerotic layer below the plug is destroyed producing a cavity that may be continuous with the hilum.

(c) Type II scarification. Partial or complete breakdown of the endostesta around the edge of the plug.

(d) Type III scarification. Breaks, fissures and cavities on the surface of the sclerotic plug.

a



c

b

d

TABLE 19: Percentage frequency in four types of seed coat scarifications in seeds of <u>P. cattleianum</u> after their passage through the digestive tracts of feral pigs in Kipahulu Valley.

Number of samples[1]	Types of seed coat scarification[2] (%)				Percent of broken seeds
	I	II	III	IV	
48	85.9 ± 9.8[3] (55 - 100)[4]	9.1 ± 8.4 (0 - 36)	3.1 ± 3.2 (0 - 12)	1.7 ± 2.3 (0 - 12)	3.9 ± 3.2[5]

[1] Each sample size consisted of 100 fecal seeds randomly subsampled from seeds extracted from a pig dropping.

[2] See text for description. Percentage frequency was based on unbroken seeds.

[3] Mean ± S.D.

[4] Range

[5] Based on total fecal seed count in 19 adult pig droppings.

micropylar plug was distintegrated either partially or completely. When the breakage was complete, a circular cavity was produced around the plug (Fig. 23c). From an examination of 48 subsamples of 100 fecal seeds the entire micropylar plug was removed from only seven seeds with Type II scarification, thus producing a circular cavity. Breaks, fissures and cavities on the surface of the sclerotic plug comprised Type III scarification (Fig. 23c), which occurred in 3.1% of gut-treated seeds examined. Type IV scarification, which was least common, showed surface scarification of the plug, but with no visible breaks or fissures. The scarified surface was usually intensely discolored (blackish).

Discussion

Fruit-eating animals acting as seed dispersers inevitably contribute to a gain in dispersal of seed plants. This is brought about by the animal eating the seeds in one place and transporting them undamaged to another place. In this way the animal not only helps to relocate seeds but can play a direct role in the introduction of the species to new environments. This study shows that the feral pig is not a predator of strawberry guava seeds but an active disperser of the plant, especially during its fruiting season. Therefore, the suspicion of Lamoureux and Stemmermann (1976) that the pig is abetting the spread of the strawberry guava is substantiated. A similar role of pigs in dispersing the common guava was reported by Judd (1936). Thus, feral pigs appear to be the primary agent responsible for the uphill spread of the strawberry guava and their actions satisfactorily account for the very dense clumps of seedlings growing in areas remote from guava stands.

Planting results suggest that pigs do not transport many seed plants on their body. Habits such as wallowing and tree rubbing would regularly free the animals of seeds at those sites. However, field observations showed that hooves were also important sites for seed collection. Although at least 16 seed plants were foods for the pigs (Chapter 6), planting of fecal materials yielded a surprisingly low seedling number and species count. Most of the seedy food plants are without hard seed-coats and, hence, may have been physically damaged by the teeth during ingestion or lose their viability as a result of passage through the pigs' digestive tracts. Hence, the feral pig does not appear to be as important in the dispersal of other seedy food plants. In Africa, the bush pig is known to feed on 26 forest tree fruits, but seeds of many of these food-plants are destroyed as a result of passage through the gut (Phillips 1926).

To assess the role of the pig as a seed disperser for Psidium cattleianum and to understand the ecological implication of this ungulate-aided dispersal, the following factors need to be discussed: fruit availabilty and its importance as a food source, gut pH and gastro-intestinal treatment, animal movements, defecation sites and frequency of defecation. All these factors interact in the establishment and distributional pattern of the plant.

In the area of this study, a major flowering season occurred from March through June and fruit fall occurred from August to December. Fruit ripening, and hence fruit drop, was non-uniform throughout this period. Thus, the fruit was available for a substantial period of the year and generally in sufficient quantity to be able to act as a primary food source for these animals during August to December.

Fruits were eagerly sought as food, particularly during the fruiting season when pigs behave as opportunistic frugivores. Movements of pigs into the fruiting area were observed to be directly related to the availability of the fruit. Four heavily used trails were monitored during this study, of which two were reopened by movements into the fruiting area. The frequency of trail use was twice each day, but no attempt was made to determine whether the same or different groups of pigs were using the trail. After the fruiting season, three of these trails were abandoned, and the trail use frequency was so low that revegetation by weeds along some sections of the trail occurred. Field observations, stomach and scat analyses showed the fruit was the principal component of the pigs' diet from September to December (Chapter 6). The dietary range was narrow during this time; the other commonly encountered food items in the stomachs being perechaetine Megascolecidae earthworms, Paspalum conjugatum, ferns, molluscs, roots and other vegetable matter.

Fruit-feeding behavior and the action of digestive fluids on the ingesta are important considerations in the preservation of seed viability. The ability of the seed to escape physical breakdown during feeding is the first determinant of dispersal. For most herbivorous mammals in Africa, seeds pass through the mammals' digestive tract without further damage (Lamprey et al. 1974), but in the impala ingested seeds were mostly damaged by the animal's smaller teeth (Jarman 1976). The ability of the seed to escape the crushing action of the teeth depends on seed-coat hardness, size of the seed, animal's dentition and eating behavior. In the case of the feral pig, ingestion did not damage the seed which has a hard seed coat. Feeding on the fruits was very brisk with minimal chewing. The occasional broken seeds were the result of jaw action and was probably accidental. Since less than 4% of the seeds were broken down, the nutritional value of the fruit was derived mainly from the pulp and not the seeds.

The higher germination value in gut-treated seeds, but similar final germination percentages in gut-treated and untreated seeds, indicate that gut passage hastens germination with no embryo mortality. The scarification of the micropylar plug--the last part of the seed to become lignified (Corner 1976)--and the erosion and breakdown of the seed-coat at these points probably facilitated the entry of oxygen and water, thereby inducing earlier germination. Acid-soaking in the gut may have brought about the release of any inhibitor substance. The stomach pH of gastric juices of the pig varies from 0.8-4.4 depending on the food and starvation level in the animal (Ryle & Porter 1959; Pond & Houpt 1978). Chemical scarification by gastric juices on ingested seeds is dependent on duration of gastric emptying, which is 6-12 hours after the last meal (Kidder & Manners 1978). Examination of gastric-treated seeds in the stomach and entire length of the digestive tract in three animals, showed that seed coat scarification was not exclusively due to gastric treatments. Bile secretions, other digestive fluids and gut microflora probably contributed to further seed-coat scarification after the initial acid scarification in the stomachs.

Hastening of germination in P. cattleianum after gut-treatment and acid scarification has also been reported in other species of guavas. Watt (1923) observed that several common guavas did not easily germinate unless seeds were derived from animal droppings. Laboratory scarification experiments using organic acids to treat the hard seed coat of the common guavas have resulted in a hastening and improved germination (Sinha et al. 1973; Singh & Soni 1974). Improved rates in germination have also been reported for some seeds recovered from the droppings of the bush pig (Phillips 1926). For many other seed plants, gut transport by vertebrates may result in enhanced germination (Ridley 1930; Krefting & Roe 1949; Lamprey et al. 1974), a hastening in germination (Swank 1944; Janzen 1970) or a lowering in viability (Swank 1944; Jarman 1976).

The potential for long distance dispersal of large numbers of viable seeds is considerable. Pigs defecate on the average 6.6 times a day (Barrett 1979 - pers. comm.). The first feces are formed and defecated 14-16 hours after a meal (Castle & Castle 1950). High fecal seed load verifies that the pig is a significant dispersal agent.

Defecation habits and rooting activity introduced other complexities in the pig-aided dispersal ecology of strawberry guava. If 20 pigs fed on the fruits for a one-month period, a total of 132 daily droppings would be scattered in their home range. If each dropping contained 2000 seeds, then there would be a total of 132 localized aggregations of 2000 fecal seeds distributed in the area. Over a 30-day period, there would be 3960 droppings resulting in 7.92×10^6 seeds. Fifty percent of these fecal seeds would have germinated in less than two weeks from the time they were dropped. Although observations of droppings containing fecal seeds along the trails were frequent, encounters with seedlings germinating from droppings were less frequent. Droppings with seeds and seedlings were frequently rooted, trampled over and buried in the ground. This observation introduces a new dimension to the dispersal ecology of the strawberry guava in that the pigs are building up a guava seed bank in their home range. Seeds in the seed bank may act as an important subsource for seed transport into new areas by rainwash.

The role of birds in exploiting the seed resource in Hawaii is well known, but its importance in seed dispersal cannot be ignored. The Chinese laced-necked dove, Streptopelia chinensis; the Indian mynah, Acridotheres tristis; the rice bird, Lonchura punctulata; the house sparrow, Passer domesticus; and the melodius laughing-thrush, Garrulax canorus; have been known to feed on the fruit (MacCaughey 1917). In Brazil, the strawberry guava is dispersed principally by birds (Oliveira 1980 Rio de Janeiro, Brazil - pers. comm.) and bats (Ridley 1930).

Birds which feed on fleshy fruit do not ingest the seeds, though seed intake may be accidental. The size of the birds is important, as small birds do not feed on the seeds. Birds with hard gizzards destroy ingested seeds; those with soft gizzards excrete seeds with their viability preserved (Harper 1977). Birds generally drop seeds in the shade. Although seed-feeding birds have been known to disperse certain plant species and help establish a forest (Janzen 1970; Smythe 1970), their role as dispersal agents, when compared to the feral pig, are probably insignificant because: (i) birds generally reject seeds, whereas whole fruits are eaten by the pig, and (ii) the stomach volumes differ in capacities; pigs can effectively transport many times more seeds in a shorter period of time than birds or other dispersal agents. Nonetheless, hollowed out and partially pecked mature and immature strawberry guava fruits have been observed. The Japanese white eye, Zosterops japonicus, has been observed to feed on the fruit; the red-billed leiothrix, Leiothrix lutea, and other birds are also known to feed on the fruit. Another animal disperser is the mongoose; seeds of strawberry guava occurred in droppings and in stomach contents of trapped mongooses.

The presently observed altitudinal range of strawberry guava in Kipahulu Valley is almost certainly not the species' potential upper limit of distribution in Hawaii. Field germination experiments in the strawberry guava-free zone at 1450m suggest that environmental conditions here are suitable for germination. Certain less favorable edaphic conditions and possible seed decay resulting from flooding in water-logged soils may limit the presently observed species range. Elsewhere, the species grows wild up to 1220m and withstands wide variations in environmental conditions. In Hawaii, salt spray and strong winds appear to diminish growth and fruit production at sea level, while cooler temperatures and low sunlight reduce growth at higher elevations (Shigeura 1973).

The principal dispersal agent of strawberry guava in the study area has been identified. The entire process of pig-assisted invasion and establishment of the weed can be observed in the field. Ingestion of the seed by pigs enhances the rate of seed germination. There is a synergistic relationship between the pig and the strawberry guava in that the pig transports the plant to new areas which in turn expands the food resources of the pig. In such a synergistic pig-plant interaction, each species helps the other to spread and colonize new habitats for their mutual benefit. In time, the entire Kipahulu Valley could conceivably be invaded and occupied by strawberry guava which will displace and exclude all other indigenous plants and dependent animals, several of which are officially declared endangered. A classical example is known on Oahu, where an extensive guava (Psidium guajava pyriferum) (sic) forest in Niu Valley Valley was established principally by feral pigs (Judd 1936). The best theoretical solution to the exotic species interaction problem would be: (i) destroy the seed source, i.e., eradicate the strawberry guava plants; and (ii) free the area of the dispersal agent, i.e., eradicate the feral pig. Eradication of strawberry guava may be sound in theory but practically impossible.

This should not be taken as a setback or an indication that the problem is insoluble. Various chemical, biological, mechanical and other cultural methods have been used in attempts to eradicate, exclude or contain the spread of strawberry guava. Some of these control measures should be adopted and integrated with a feral pig control program. Control programs aimed at eradicating the pig or depriving it of strawberry guava as a food source may be more practical, at least initially.

The type of exotic species interaction described in this study plagues managers of native ecosystems and once again carries a special message to Committees on Animal Importation. Introduced animals interact to produce obvious or subtle relationships and consequences that could change with time and habitat, causing undesirable effects which are ecologically disdvantageous to man and natural ecosystems. Animals should be introduced into new areas only after the most careful evaluation of their potential impact.

Finally, it is hoped that this study will arouse interest in future research on effects of internal seed passage through herbivorous and granivorous animals. In Hawai'i, information of this nature would be valuable for range, forest and wilderness management.

CHAPTER 8

POPULATION CHARACTERISTICS

Introduction

Several population parameters (density, age structure, reproduction and movements) are commonly used to model the growth of wild pig populations (Tipton 1977, 1980). These data are usually obtained by interpreting capture-recapture records and statistics of individual animals derived from a live-trapping program. The interactions among these parameters in mammal populations are also evident. Density, for instance, influences group size and trapping success while dispersal patterns and fluctuations in reproductive efficiency modify the age-sex composition in wild pig populations (Singer 1977; Singer et al. 1981).

The purpose of this phase of the field study was to obtain basic information on population parameters in order to plan the management of this feral pig population. A livetrapping program was used to: (i) determine the trappability of pigs in the different forest types, (ii) evaluate the feasibility of live-trapping as a control tool, (iii) determine the most effective bait, and (iv) estimate population density by mark-recapture methods. Secondarily, the trapping program will provide animals for describing population age structure and trap revealed movement patterns which might supplement home range results from radiotracking studies.

Materials and Methods

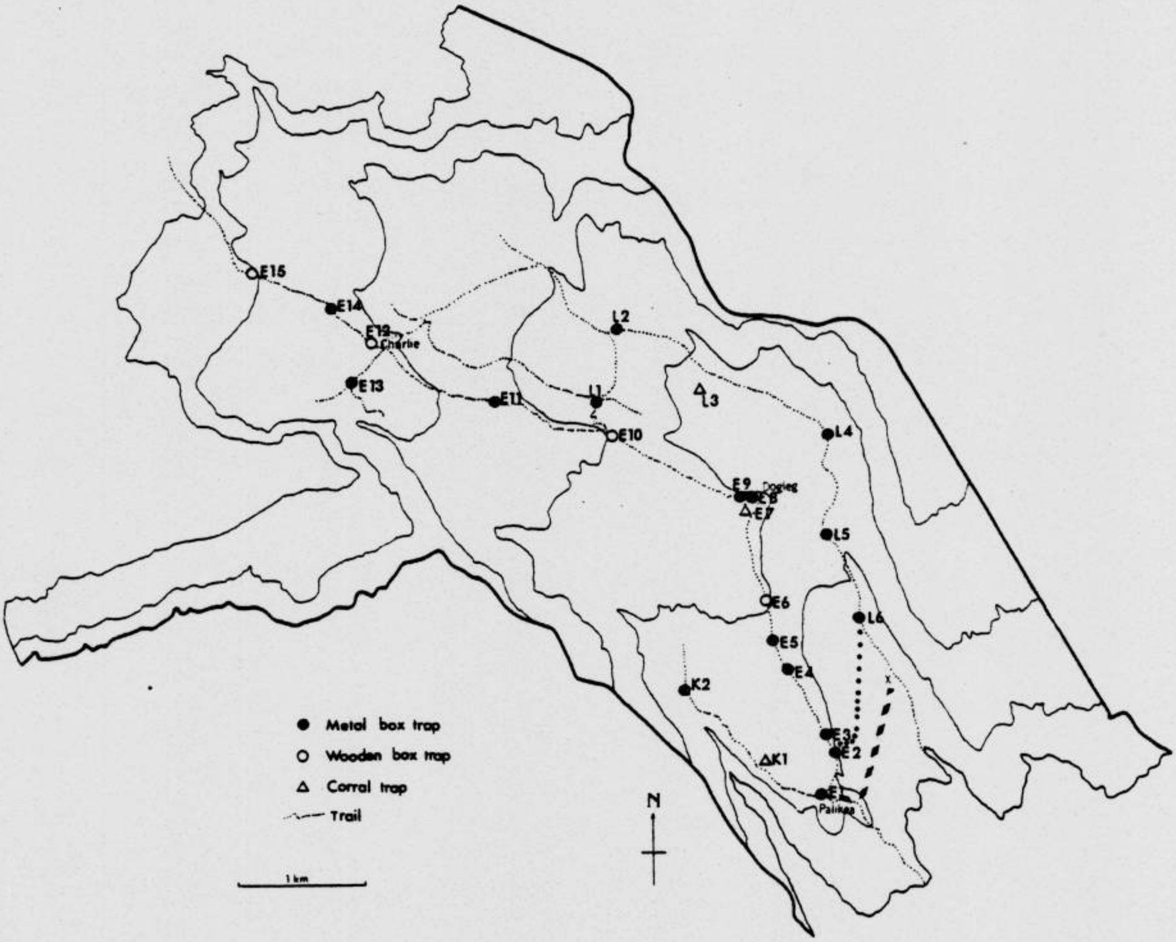
(a) Livetrapping techniques

Traps were sited on the central escarpment (E), Koukouai (K) and lower plateau (L) trails (Figure 24).

Trapped animals were manhandled with a neck-noose, the free end of which was adjusted such that the running radius of the lassoed animal from the trap door was not more than a meter. Animals were approached from the rear; one of the hind legs was tied to the side of the trap before tying together the other legs and jaws, and freeing the restrained animal of its neck-noose. Pigs less than 40kg were manhandled using the method described by Barrett (1971); this author used his handling method for adults up to 70kg. With multiple captures, animals were individually roped and released one at a time for restraint. Roped animals were occasionally released from both the door and rear end of the trap. Two immobilants, etorphine hydrochloride (D-M Pharmaceuticals, Inc., Maryland) and succinylcholine chloride (Burroughs Wellcome Co., North Carolina), were sometimes used. Immobilants were administered intramuscularly in dosages of 0.65-0.85mg/kg body for the tranquilizer (Wood et al. 1977) and 0.04mg/kg for the narcotic.

Traps were usually baited with whole kernel corn, coconuts or hapuu (tree fern logs). These, together with three other baits [ieie (Freycinetia arborea), beef scraps and pig carcass], were field tested and observed for their effectiveness, nuisance problem and bait life. A bait was scored as effective if capture occurred simultaneously with a

Figure 24: Location of corral and box traps in Kipahulu Valley. ▬▬▬▬▬ movement route for a pig trapped in E1 and shot by a hunter at X; ...... movement route for a pig trapped in E2 and recaptured in L6.


E15
E14
E12
Charlie
E13
E11
L2
L1
2
E10
L3
L4
E9
Dogleg
E8
E7
L5
E6
L6
E5
E4
K2
x
E3
E2
K1
E1
Palikea
N
● Metal box trap
○ Wooden box trap
△ Corral trap
Trail
1 km

visit, i.e., observations of rooting activity within an area of radial distance 15m from the trap.

Traps were usually inspected one or two nights after baiting. Those at the extremities of the trapline (E15, L6) were sometimes inspected after three nights, and in these, the recency of tracks at trap sites was used to estimate the night of capture. Trapping effort was expressed as trap nights. Trapping success at trap sites, per month and for each forest type, was calculated as the number of pigs trapped per 100 trap nights. The different trap designs are shown in Figure 24.

Pigs were marked on both ears with two types of numbered, color-coded, double-holed-lock tags, in an attempt to ensure a mark-recapture density estimate assumption that marked animals stayed marked during the sampling period. Eartagging was done by first sandwiching the outer rim of the anterior earlobe with a tag such that the numbered surface faced upwards and the tag's connector was flush with the ear margin, and then locking the tag in position with a Salasco "All in 1" (Nasco West, California) compound lever pliers. Recaptured animals were recorded for their tag numbers, recapture date and trap location. Mark-recapture data were used to describe trap-revealed movement patterns and estimate density.

In order to determine the optimum period between trap inspections, four trapped pigs were continuously observed from initial capture to death in the trap.

(b) Population estimates

Population size was estimated by analyzing mark-recapture data with the following estimators: Schnabel (1938), Schumacher-Eschmeyer (1943), Jolly-Seber method (Caughley 1977) and the frequency of capture models (Caughley 1977). Calculations were performed on a trap-day basis as well as for each monthly trap session. The latter approach assumes each trap session as one trap "day." The assumption of equal catchability was tested by comparing the variance of trap data to that of a binomial expectation using a X^2 test (Caughley 1977).

(c) Age determination

Pigs younger than 36 months were aged by tooth eruption and replacement sequence (Matschke 1967; Barrett 1973). Dentitions were examined with a mouth speculum and animals were assigned into Matschke's age class. Visible crown height and tooth wear were further used to age the animal to its nearest month. Animals from 24-36 months were aged using the following dental characters: sequence of cuspal eruption in M3, relative degree of exposure and coalescence of exposed dentine, and loss of tooth structure. Animals were aged as 24, 28 and 32 months at the appearance of the first, second and third pair of cusps, respectively; their ages being estimated as 36 months when M3 was fully erupted. Four-year olds were aged respectively as 40, 44 and 48 months at the appearance of a complete enamel ring, coalescence of exposed dentine with visible signs of dentinal erosion and by the relative loss of tooth structure. Five-year olds were aged as 52, 56 or 60 months using the following dental characters: relative degree of attrition, relative loss of crown height and loss of at least one tooth. Animals edentulous in their molar and premolar regions were aged as 72 months. Dental characters used to age pigs older than three years were subjective and assumed attrition and loss of tooth structure to be linear functions of chronological age.

(d) Survivorship and fecundity patterns

A crude survival curve was constructed using the data on age-sex composition. Survivorship (1_x) between age intervals was calculated as N_x/N_o; N_x was the number of individuals in age class x, and N_o the number of individuals in the zero age class. An adjusted survival curve was generated by calculating 1_x at 6 months. The mortality rate at 6 months was estimated using the difference between the litter size at birth and the number of lactating (functional) nipple count, and sows (N=6) with recent loss of their entire litters. Survivorship from 6 months to one year was obtained by interpolation using the corresponding slope in the crude survival curve, i.e. the percent of the cohort surviving from one to the two-year age interval. This procedure was used to estimate survivorship for the subsequent age intervals in the adjusted 1_x curve. Age-specific fecundity was calculated by first estimating the incidence of pregnancy (I) in the sample population, following the methods illustrated by Caughley (1978), and then multiplying it by one-half the litter size at birth, since a 1:1 sex ratio was assumed. The overall net reproductive rate, R_o, was calculated as $R_o = \sum_{x=0}^{6} 1_x m_x$.

(e) Collection of reproductive data

Sows trapped during the mark-recapture study were visually examined for their reproductive condition and recorded as pregnant or nonpregnant. In lactating animals, the number of functional nipples were counted and used as an estimate of the number of surviving offspring. This functional nipple-offspring correspondence assumes that one piglet will suckle one same nipple throughout the preweaning period. In 1980, necropsies were performed on 16 shot and 12 live-trapped sows to collect reproductive tracts and their ovaries. Presence of spermatozoa in the epididymis was used as a criterion for sexual maturity in boars. Reproductive tracts were dissected in the field and fetuses were counted, sexed and measured. Fetuses were aged using crown-rump length measurements, following Warwick (1925) and Henry (1968). Farrowing dates of fetuses collected from individual sows, as well as birth date of animals less than a year old captured in the mark-recapture study, were calculated and represented with a frequency plot to examine if there were seasons of birth. Ovaries were serially hand-sectioned following a method parallel to Barrett's (1971), and microscopically examined for counts of the corpora lutea. The consistency of luteal cells was used as a criterion to distinguish corpora lutea from other follicular structures (Corner 1915). Reproductive data were used to estimate (i) prenatal mortality by comparing corpora lutea counts with fetal count, and (ii) postnatal mortality by comparing litter size at birth and weaning.

(f) Group size

Group size data were recorded while hiking on trails through the Valley and also from two tree blinds. Groups were usually watched until they dispersed. Recency of tracks and ground disturbance were often helpful in detecting and homing in on a group. Pigs usually vocalize and remain still momentarily before moving away whenever alerted by human presence. This behavior pattern further assisted in group detection. Several groups were, however, sighted in their undisturbed state. Sightings were within 30m, with most of them not more than 15m. Sexing was not always possible because of the dense vegetation. Thus, only the numbers in a group, group type and sighting location were recorded. Group size was expressed as a mean value and with a frequency distribution.

Results and Discussion

(a) Livetrapping

(i) Trapping success.—From July 1979 through March 1980, there was a total of 108 captures and recaptures involving 76 pigs. These captures came about from 65 closures of traps which were set for a total of 938 trap nights in the koa forest and 232 trap nights in the ohia forest (Table 20). In another trapping season on the lower plateau, extending from April through November 1980, 20 pigs were caught in 11 closures with an effort of 352 trap nights. Thus, a total of 1522 trap nights during a 17-month period resulted in a total catch of 134 pigs from 76 captures or 1.79 pigs per capture and a trapping success of 8.8

TABLE 20: Trap-night data for 136 feral pig captures and recaptures in Kipahulu Valley from July 1979 through November 1980.

Forest type	Month	Traps available/set	Trap Nights	Captures	New Captures	Recaptures	Total number of pigs	Trappability[1]			
								Captures	New Captures	Recaptures	Captures & Recaptures
Upper plateau Koa forest	July 1979	K1 E1-3, 5-10	134	4	5	2	7	2.9	3.7	1.5	5.2
	August	K1 E1-3, 5-10	110	9	11	0	11	8.2	10.9	0	10.0
	September	K1 E1-3, 5-10	106	12	14	4	18	11.3	13.2	3.8	16.9
	October	K1 E1-3, 5-10	114	5	5	3	8	4.4	6.1	3.5	7.0
	November	K1 E1-3, 5-10	95	12	14	4	18	12.6	14.7	4.2	18.9
	December	K1 E1-3, 5-10	79	5	6	8	14	6.3	7.6	10.1	17.7
	January 1980	K1 E1-3, 5-10	98	2	3	4	7	2.0	3.1	4.1	7.1
	February	K1-2 E1-10	74	4	4	7	11	5.4	6.8	9.5	14.9
	March	K1-2 E1-10	128	7	9	5	14	5.5	7.8	3.9	10.9
		x̄	938	60	71	37	108	6.4	7.6	3.9	11.5
Upper plateau Ohia forest	July 1979	E12-13, 15	16	0	0	0	0	0	0	0	0
	August	E12-13, 15	26	1	1	0	1	3.8	3.8	0	3.8
	September	E12-13, 15	18	0	0	0	0	0	0	0	0
	October	E12-13, 15	27	2	2	0	2	7.4	7.4	0	7.4
	November	E12-13, 15	40	0	0	1	1	0	0	2.5	2.5
	December	E12-13, 15	36	0	0	0	0	0	0	0	0
	January 1980	E11, E12-13, 15	20	0	0	0	0	0	0	0	0
	February	E11-15	27	1	1	0	1	3.7	3.7	0	3.7
	March	E11-15	22	1	1	0	1	4.5	4.5	0	4.5
		x̄	232	5	5	1	6	2.2	2.2	0.4	2.5
Lower plateau	April 1980	L1-6	60	0	0	0	0	0	0	0	0
	May	L1-6	70	1	2	0	2	1.4	2.9	0	2.9
	June	L1-6	44	0	0	0	0	0	0	0	0
	July	L1-6	36	3	5	1	6	8.3	13.9	2.8	16.7
	August	L1-6	22	2	2	0	2	9.1	9.1	0	9.1
	September	L1-6	38	0	0	0	0	0	0	0	0
	October	L1-6	42	4	6	2	8	9.5	14.3	4.8	19.0
	November	L1-6	40	1	1	1	2	2.5	2.5	2.5	5.0
		x̄	352	11	16	4	20	3.1	4.5	1.1	5.7

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[1] per 100 trap nights

pigs per 100 trap nights. Overall trapping success per 100 trap nights for captures and recaptures averaged 4.9 and 2.8, respectively. Trappability was, however, highest in the upper plateau koa forest (12.2 pigs per 100 trap nights) and lowest in the ohia forest (2.5 pigs per 100 trap nights). In the koa forest, trappability was highest in November. Monthly variations in trapping success is apparent from the data.

(ii) Trap location and visitation.—Trappability index varied considerably among trap sites (Table 21) and is highest at E4. A total of 281 visits to 23 trap sites occurred in 1522 trap nights. Thus, the trap site visitation frequency was only 17.5% of the trap nights. Koa forest traps had the highest visitation frequency (23.8 visits per 100 trap nights); this index was 5.5 times and 3 times lower for traps in the lower plateau and ohia forest, respectively.

(iii) Baits.—Baits differed in their attractiveness to pigs visiting a trap site. Among the four plant baits tested from July to September 1979, hapuu had the highest baiting success (83.3 captures per 100 trap visits) (Table 22). Bait success for corn was higher than for coconut. Meat-baited traps produced no captures. Visiting pigs showed no interest in pig carrion, as was frequently evidenced by trails that stopped short or went past the entrances of such traps. Only one carcass from 12 of 22 pigs shot in 1980 was known to be consumed, and the bones of four others were gradually eaten over a period of several weeks. Carrion from four animals in the trapped animal survival test

TABLE 21: Visitation frequency and trappability data of feral pigs at individual trap site from July 1979 through November 1980.

Variables	Traps																							
	K		E															L						
	1	2	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	1	2	3	4	5	6	TOTAL
Trap nights	65	24	106	88	88	20	88	84	80	92	105	98	28	74	56	22	52	54	86	46	60	54	52	1522
Visits	4	2	7	10	9	5	6	4	5	7	7	5	2	1	1	0	1	2	5	2	2	3	2	92
Captures	4	1	3	5	4	2	4	2	4	3	2	3	1	0	0	0	0	0	2	0	0	2	0	42
Recpatures	8	3	10	15	13	7	10	6	9	10	9	8	3	1	1	0	1	2	7	2	2	5	2	134
Total catch	10	3	19	22	28	7	18	24	14	28	36	14	3	4	3	2	6	6	10	7	5	5	7	281
Trappability	12.3	12.5	9.4	17.1	14.8	35	11.4	7.1	11.3	10.9	8.6	8.2	10.7	1.4	1.8	0	1.9	3.7	8.1	4.3	2.3	9.3	3.8	8.8

TABLE 22: Relative effectiveness of food baits expressed as the number of captures per 100 visits to a trap site. Study period extends from July through November 1979.

Variable	Bait					
	Hapuu[1]	Corn[2]	Coconut	Ieie[3]	Pig Carcass	Beef scraps
Trap nights	84	82	52	20	64	18
Number of visits	18	15	20	10	12	4
Number of captures	15	8	9	2	0	0
Bait success[4]	83.3	53.3	45	20	0	0

[1] Tree ferm (*Cibotium* sp.) core

[2] whole kernel

[3] woody vine, *Freycenetia arborea*

[4] captures per 100 units

did not self-bait any pig even though activity was recorded from within the bait recognition area.

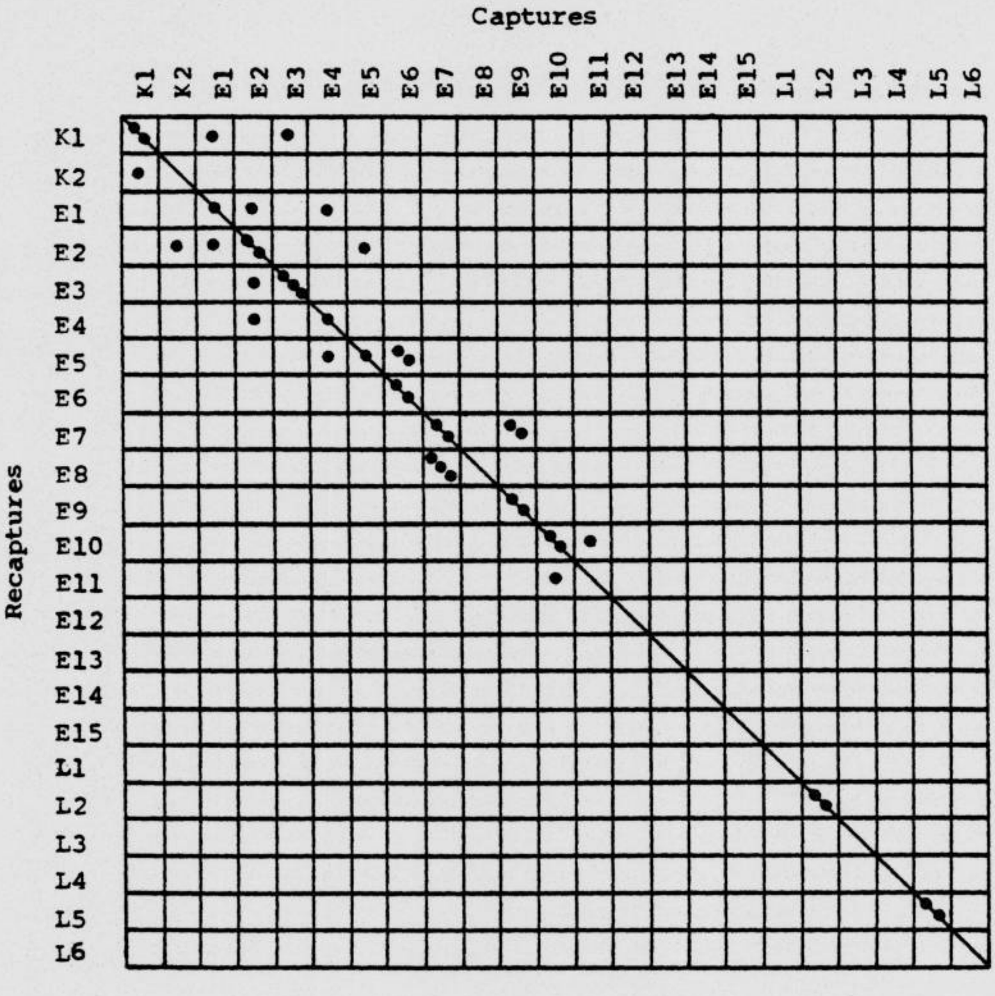
Baits differed in their physical characteristics. Field observations show that baits lose their effectiveness when they turned mouldy (hapuu), rancid (coconuts), browns or decays (ieie and corn). Hapuu and corn had a bait-life of 5-8 days, coconuts 3-6 days and ieie 3-5 days. Rebaiting at some trap sites was necessary whenever corn or coconut were used as baits. Rats readily consume these baits, particularly coconuts. Hapuu was the most suitable bait in traps whose floors were temporarily flooded or covered over by a mud pool. Corn was the most unsuitable bait under these circumstances and was often buried by mud from rainwash.

(iv) Trap design.—Twenty-two out of 23 traps (95.7%) were successful in at least one capture (Table 21). The root-bar trigger system and the baiting techniques were highly sensitive and successful. All bait consumption at the root-bar trigger resulted in captures. Trap design alone did not affect trap success. Only 6 escapes (one at E11, four at E7 and one at L3) were recorded out of 134 captures and recaptures. Escape at E11 was by a piglet squeezing itself between the crossbars in the rear panel. Two of the four escapes at E7 were through cavities at the base of the tree around which E7 was constructed. The remaining escapes were by door-lifting. Trigger avoidance in drop-door design was recorded in seven out of 18 visits at E6. Pigs avoided the trigger string to feed on the bait (hapuu or coconut) in the trap and took the bait out of the trap for consumption. Entry reluctance was seen whenever the trap floor sank or the trap was fronted by a mud pool. Rainwash in combination with animal tramping sometimes compacted or removed the ground under the floor of the trap. When the floor fabric was off the ground, approaching animals exhibited trap wariness, consumed the bait at the door or inside front end of the trap, but never moved into the rear of the trap. Wariness was counteracted by either resiting the trap or shovelling soil onto the floor of the trap.

(v) Behavior of pigs in response to traps.—Track signs and partially consumed bait at trap sites, gave useful clues on the responses of feral pigs to baits and capture devices. Five trap behaviors were identified during the 17-month trapping period. The most commonly observed trap behavior was trap-habituation. This involved pigs recaptured more than once in a neighbouring trap or the trap in which they were first captured. Locations of all recaptures in relation to their first capture site are as shown in Figure 25. Among recaptures, 52.4% were recaptured in their first capture site. Two piglets first caught at E6 and E7 were each recaptured four and five times, respectively, over an eight-month period.

(vi) Trap-revealed movement patterns.—Mark-recapture data did not reveal any movements between koa and ohia forest pigs (Figure 25). The longest linear capture-recapture distance (E13-E11, K2-E3) was 1.12km. Recapture directions tended to be unidirectional for longer inter-trap distance and bidirectional when between traps with narrower distance. Inter-plateau movement was revealed by one recapture record. A sow (2042-17) captured and released at E1 on November 20, 1979, was shot by

Figure 25: Capture and recapture locations (trap sites) for all feral pig recaptures during the mark-recapture study from July 1979 to December 1980, in Kipahulu Valley, Maui. Alphanumerals on the matrix denote the position of a box or corral trap on a particular trail system (cf. Figure 24). K1, K2, E1 to E10 - koa forest traps; E11 to E15 - ohia forest traps; L1 to L6 - lower plateau traps. Closed circles on any square in the matrix show capture-recapture orientations, i.e. the trap in which a pig was first captured and subsequently recpatured. Pigs recaptured in the traps in which they were first captured are represented by closed circles on the diagonal of the matrix.


Captures
K1
K2
E1
E2
E3
E4
E5
E6
E7
E8
E9
E10
E11
E12
E13
E14
E15
L1
L2
L3
L4
L5
L6
Recaptures
K1
K2
E1
E2
E3
E4
E5
E6
E7
E8
E9
E10
E11
E12
E13
E14
E15
L1
L2
L3
L4
L5
L6

a hunter at X on the lower plateau. The recapture distance E1-X was 1.04km. E2-L6 was the only other recapture distance for a pig trapped in E2 and recaptured in December 1980 in E6; the recapture distance was 1.10km. Probable movement routes for these two pigs are as shown in Figure 24.

(vii) Survival in trapped animals.—From September through December 1980, four trapped animals, two in E3 and one each in E4 and E11, were continually observed from day of first capture to death in the trap. Experimental animals were between 45-70kg. Weather during the study period was mostly cloudy with variable winds and light to heavy intermittent rains.

The ohia forest pig died five days after capture. Koa forest pigs averaged 6.7 (5-8) days survival in the trap. Experimental pigs became less active with starvation time. Body tremor occurred on day 3-5 after capture. Therafter, the pigs sat on their hind legs and then crouched on their fore legs at a corner or leaned against a side of the trap. Acute withdrawal behavior was shown with the onset of crouching. Experimental pigs did not attempt to leave the trap even when the door was left open and resisted being dragged out. Death occurred about 2-3 days after the onset of the withdrawal behavior.

Trapping success has been quantified in units such as trap nights per pig, rates of success and pigs per trap night (Conley et al. 1972; Fox & Pelton 1977; Singer 1977). The trappability index used in the present study is similar to the rates of success used by Fox and Pelton

(1977) in that it avoids differences in total catches caused by differences in the number of available traps, or times they were used. Using trap nights per pig as the basis for comparing success, it can be seen that overall trap success in Kipahulu Valley (8.8 trap nights per pig) is higher than those reported by Singer (1977) (14 trap nights per pig) or Fox and Pelton (1977) (47.5 trap nights per pig) from two wild boar populations in Tennessee. The latter author discounted live-trapping as a control tool in his study area at that low trap success. The higher trap success in the Valley can be attributed to its relatively denser population, particularly in the lower elevations.

These data suggest that trapping is a more feasible control method in koa than ohia forest. Trap success in koa forest averaged 8 trap nights per pig whereas that in the ohia forest was 35 trap nights per pig.

Variability in the trappability index among upper plateau koa, upper plateau ohia forests and the lower plateau can be attributed to two sets of factors: (i) population, and (ii) experimental. Pig density is highest (see below) in the koa forest and this invariably contributes to higher trapping success. This habitat is preferred over ohia and lower plateau areas because maintenance needs of food and shelter are more readily available and superior to those in other areas. Trap-associated behaviors and meat baits will lower trappability by reducing total catch relative to an increase in the number of trap nights.

Inefficient trap designs and high number of escapes contributed to the low trapping success in a wild boar population in Tennessee (Singer 1977). In the present study, traps and baits were considered effective because of the high ratio of visits to recaptures. The drop-door design such as that in E6 was, however, troublesome, but the design and the root-bar trigger system on all other box traps were effective in catching and holding the catch. The use of three different food baits, each with differing baiting success, most likely introduced some bias into the trappability index. Field baiting experience strongly suggests that tree fern core can effectively increase trapping success, as was borne out in its high baiting success, and a 1:1 visit:capture ratio is possible if baiting was correctly done in traps whose inhibitions for entry had been corrected.

It is felt that trapping success, particularly in the koa forest, could have been higher if method-related influences had been manipulated. Escarpment traps do not have a maximum area of influence. If an area of trap influence is drawn using each trap as the center of areal influence, it can be seen that only about 50% of the trap's area of influence is available to catching pigs from the upper plateau. Thus, escarpment traps are available only to pigs when they move out from the interior of the plateau. The low trap visitation frequency can be explained by the fact that existing traplines are sited on home range peripheries and away from the activity centers of the ranges. The probability of capture, and hence trapping success, can be expected to increase when traps are placed closer to the animal's activity centers

(Harrison 1958). At the outset of the study, it was thought that pigs moving out from the interior of the plateau to the escarpment will move long distances up or down the escarpment ridge. This was not the case (Chapter 9); thus, existing trap locations were not effective in intercepting such movements. When live-trapping is to be used as a control tool, it would be necessary to consider the deficiencies of existing traplines and explore methods of increasing trap success by increasing the trap's area of influence and visitation frequency to the traps.

(b) Population estimation

Population size was estimated with mark-recapture data collected from two trapping seasons (Table 20). A total of 76 pigs were marked on the upper plateau koa and ohia forest over 9 successive monthly trapping sessions. In the lower plateau, 16 pigs were marked during 8 trapping sessions. Handling and eartagging techniques brought no known mortality to the experimental animals.

On the upper plateau, only 27.6% (21) of the marked pigs were recaptured at least once (Figure 26). The most common recapture frequency was two, and this category accounted for 31.6% (12) of the total 38 recaptures. One pig, first caught in August 1979, was recaptured five times, once each in December 1979, January and February 1980, and twice in March. Recaptures were of two kinds: (i) within session recaptures referring to those pigs retrapped within a trap session, and (ii) between session recaptures, referring to those pigs

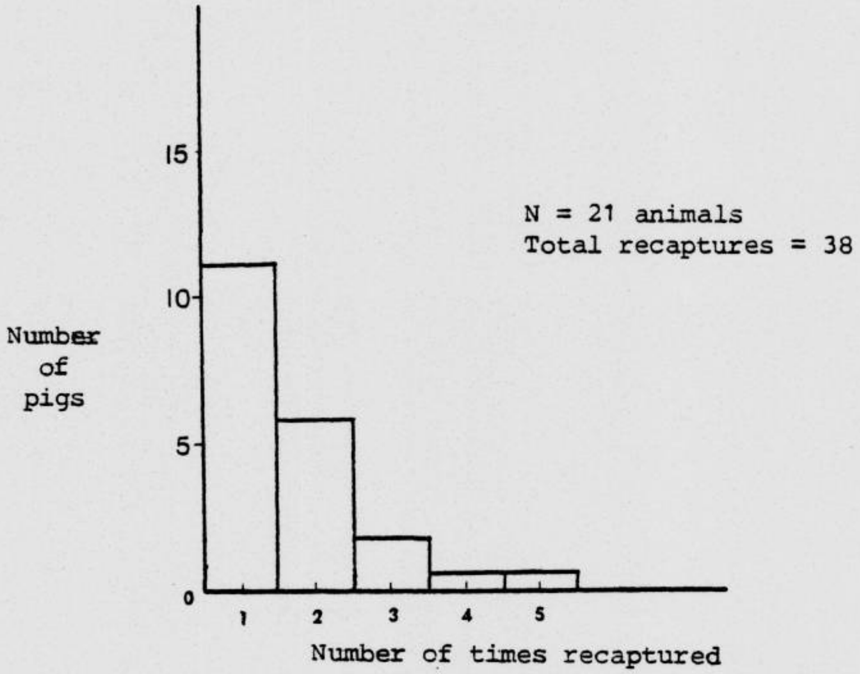


Figure 26: Recapture frequency for feral pigs tagged and released on the upper plateau, Kipahulu Valley, Maui.

caught in a session but which were marked in a previous session. Considering all recaptures from both plateaus, 52.4% (22) of the total recaptures occurred in the traps in which the pigs were first caught (Figure 25).

The hypothesis that catchability was constant was tested by comparing the variance of the capture-recapture data to that of the equivalent binomial expectation. Observed variance differed significantly from expected binomial variance ($X^2=161.5$, df=75, $P<0.001$). Thus, the population was not sampled at random.

Population size was estimated individually in each of the three geographic areas: ohia, koa forests and the lower plateau. This subdivision coincided with pig distribution and habitat heterogeneity. In the ohia forest, density estimation was not possible because of too few captures. Based on track counts, the density in the ohia forest was estimated at 4.8 (0 to 8.5) pig per km^2. Lincoln estimators gave unrealistically low estimates in the koa forest when density was estimated using trap-day data. Recapture data were too scanty for application of the Jolly-Seber method. If trap sessions data were used in the Jolly-Seber model, estimates would have been unrealistic because there were too few recaptures. The frequency of capture models gave unrealistically low estimates.

The Schnabel and Schumacher-Eschmeyer methods gave meaningful, realistic and very similar population estimates (Table 23). The most reliable Schnabel estimate is for the March trapping session. The

TABLE 23: Population size of feral pig by trapping session estimated by four methods

Estimators		Population size estimates (N)								
		Upper plateau koa forest								
		July 1979	Aug	Sept	Oct	Nov	Dec	Jan 1980	Feb	March
Schnabel	N	--	∞	295	113	160	131	127	125	138[1]
	C.I.[2]	--	--	inadmissible	60-1079	91-645	85-292	113-145	87-225	99-235
Schumacher-Eschmeyer	N	--	55	196	87	151	120	118	117	135
Jolly-Seber	N	--	132	336	108	1008	78	∞	13	--
	S.E.	--	∞	356	78	1204	54	--	5	--
Frequency of capture		Poisson estimate			Negative binomal estimate				Geometric estimate	
	N	30			36				46	
		Lower plateau								
		Apr 1980	May	June	July	Aug	Sept	Oct	Nov	
Schnabel	N	---	---	---	12	∞	---	33	32	

[1] most reliable estimate

[2] 95% confidence interval

population size is estimated at 138 pigs (30.7 pigs per km^2) and a 95% confidence range of 99 to 235 pigs. The lower plateau density is estimated by the Schnabel method as 8.2 pigs per km^2.

Density estimators used in this study belong to two general classes: (i) variations of Lincoln index-the Schnabel (1938), Schumacher and Eschmeyer (1943) and the Jolly-Seber mark-recapture estimators which are based on the Poisson distribution, and (ii) the frequency of capture models. For the density estimates to be reliable it will be necessary to assess whether the mathematical assumptions (Caughley 1977) in the models were met during the study.

(i) Marked pigs remained marked throughout the trapping season.—Two of the total 28 marked pigs that were recaptured at least once, lost one but not both eartags. Thus, all recaptures were identifiable.

(ii) Marked and unmarked pigs die or leave the valley at the same rate.—There is probably no differential mortality between marked and unmarked pigs. Marking caused no injury. All trapped pigs were visibly healthy. There was no evidence of emigration, although dispersal movements were detected at the mouth of the Valley in one instrumented pig.

(iii) No pig is born or immigrates into the Valley between marking and recapture.—There was no known immigration, but there was evidence of recruitment. Recruitment dilutes the number of marked pigs and increases the population estimate.

(iv) The probability of capturing a pig is the same for all pigs in the population.—Catchability was unequal, and this can be attributed to several factors.

Observation of unmarked pigs between trap locations suggests that traps would have to have been repositioned to intercept the movements of some pigs. Capture opportunities among traps were not equal because of the geography of trap locations. The upper plateau widens from 0.5km at its base to its greatest width of 1.5km at mid-elevation before continuing to narrow upslope. Thus, with the existing trapline, the probability of capture will be higher in the narrower than broader segments of the plateau. Habitat heterogeneity and movement patterns may have contributed to unequal catchability. Restricted home range limits random mixing. Trap-associated behaviors may reduce or increase capture probability depending on whether trap-shyness or trap-habituation was the case. The low proportion of recaptures suggests that initial capture and handling may have reduced inherent catchability (Singer 1977).

Among the mark-recapture estimators used, only the Schnabel and Schumacher-Eschmeyer methods accumulate captures and recaptures for population size estimation. Low recaptures and scanty data make the Jolly-Seber method unsuitable. This was also noted by Singer (1977) when he attempted to estimate density of the wild boar in Tennessee.

The frequency-of-capture model estimates population size by estimating the frequency of the zero-class in truncated frequency distributions of number of animals caught once, twice, thrice, etc. (Caughley 1977). The models are based on different assumptions of catchability. The Poisson estimate assumes constant catchability, while the binomial and geometric estimates allow for different types of catchability. All three models gave unrealistically low estimates. This is most likely due to some pattern of unequal catchability not provided for in these models, which Caughley says does not cover an "exhaustive list of possible ways in which catchability varies." Caughley further pointed out that these models do not estimate population size if animals die over the trapping season or when the population is open.

The Schnabel estimate of N is biased downwards because of unequal catchability. If assumptions 1 to 3 are violated, N will be positively biased. Since assumption (1) is met in full, any positive bias will be due to population recruitment during the trapping season. When this positive bias overcompensates for the negative bias due to unequal catchability, N will be an overestimate. The present data do not allow this to be evaluated. The population size (N) is, however, a reasonal estimate but not precise, perhaps, for works on population dynamics. Robson and Rieger (in Begon 1979) recommends a 0.5 accuracy (true N in range of 0.5N to 1.5N) for preliminary or management studies. Based on this, the koa forest density ranges from 15.3 to 46 pigs per km^2.

The usefulness of mark-recapture methods for population size estimation has been questioned. Singer (1977) firmly recommends against using these methods, citing inappropriateness of the model assumptions, unreliability of estimates and the high cost involved in collecting mark-recapture data. Giffin (1978) found the Lincoln index unsuitable for estimating feral pig density in rainforest habitats on Hawaii.

For this study, the Lincoln index was thought appropriate for the relatively small and essentially enclosed valley. Sampling was, however, not random and this is due to the arrangement of the traps and the geography of the Valley. If the Valley floor had been one large continuous area the behavior and movements of the pigs would have been more consistent with the assumptions of the mark-recapture techniques.

Despite the rigidity of the model's assumptions, mark-recapture studies have a place in field ecology for providing other useful information about the population, as is demonstrated in this study.

(c) Age-sex composition

The population structure is described from a total of 122 animals examined from July 1979-June 1980. This sample was comprised of 76 trapped, 34 shot and 12 hand-caught animals. Shot category consists of 24 lower-plateau pigs harvested by Kipahulu and Hana hunters and those experimentally shot for other aspects of this study. The number of hunter-killed animals did not represent total annual harvest. Only animals examined for their jaws were included in the sample.

The oldest animal was a toothless sow, aged as 72 months (Figure 27). The mean age of the population was 19.1 months, while the median age was 16.2 months. Young (less than 1 year) made up 41.7% of the

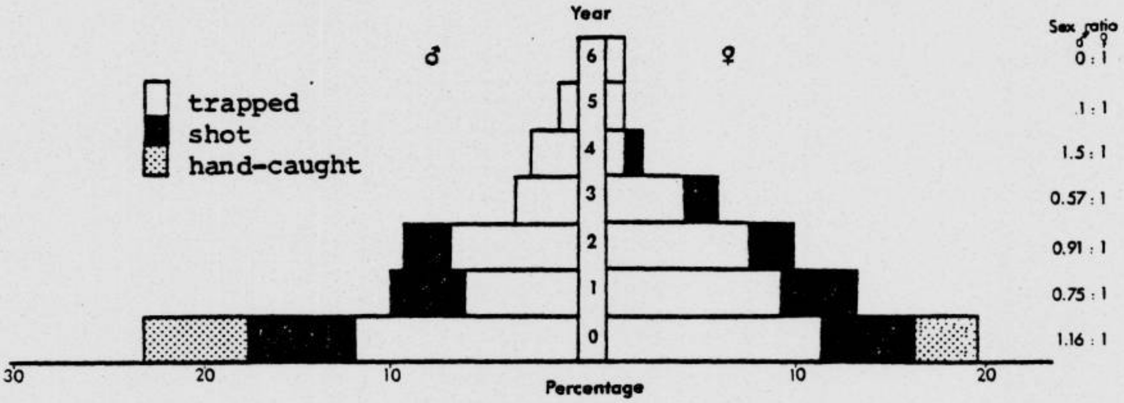


FIGURE 27: Age-sex composition of 122 feral pigs in Kipahulu Valley. Sample population covers a period from July 1979 to June 1980 and is derived from captured, shot and hand-caught animals.

population, yearlings 22.9%; the proportion of young was nearly equal to that for yearlings and two-year olds. Four-year olds and older age classes made up only 6.4% of the sample population. The crude sex ratio, expressed as the proportion of females to total animals, was 0.52 ± 0.09 (Binomial confidence interval, n=122). Variation in age-specific sex ratio was apparent. The young:adult ratio was 0.23:1. The male:female:juvenile ratio was 2.6:2.8:1, the juvenile:total population was 1:5.3 and the adult female (5 months or older):total population was 1:2.25.

The capture and harvest methods might have produced some bias in the age-sex data. Hunter-derived specimens were mostly adults from mixed groups, whereas trapped animals mostly involved individual members in a group. Continuous observations of free-ranging groups during the entire study period suggest that the sample age structure is representative of the population. The closure of the age and structure at 72 months was realistic, but contrary to initial expectations for even older and a greater proportion of older animals. Tooth loss from dento-alveolar diseases and attrition was the most important source of adult mortality which limits physiological longevity and consequently the maximum age of adults. Variations in age-specific sex ratios were most likely due to the smaller sample size in the older age class, but differential sex mortality is possible. The median age is probably a better descriptive population parameter than the mean and indicates that the population is relatively young. All the age-sex ratios suggest high juvenile mortality and a low sow reproductive (rearing) success.

(d) Survivorship and fecundity patterns

Both the crude and adjusted survival curves gave a similar mortality pattern (Figure 28). The survival curve was characterized by very high juvenile mortality (60%) from birth to 6 months and high mortality among adults in their second year. The sow's fecundity varied with age. The m_x value was highest for the two-year olds (Table 24). The instantaneous net reproductive value, R_o, was 1.24, indicating that the population was relatively stable.

Population survival curves for natural populations of the feral pig and the wild boar are exponential and characterized by high piglet mortality (Jezierski 1977; Barrett 1971, 1978). These general mortality patterns are borne out in this feral population, as shown by the ajusted curve which is considered more realistic than the crude survival curve.

With reference to the adjusted survival curve, the sources of mortality identified for this population (Chapter 11) may be grouped into those which act on: (i) young less than six months old, (ii) adults in their second year, and (iii) older animals, limiting their maximum life span. Flooding of farrowing nests, inadequate rain shelters and early evacuation from such shelters are important sources of piglet mortality in this rain forest habitat since piglets less than one month old cannot thermoregulate effectively (Myrcha & Jezierski 1972). Entrapment in mud and accidental abandonment are other sources of piglet losses. Aside from these habitat factors, predation by the mongoose is likely to be an important source of juvenile mortality since igure 28: Crude and adjusted survivorship curves for the feral pig population in Kipahulu Valley. $l_{x(a)}$ - crude survivorship curve, plotted using the age-sex composition data in the sample population; $l_{x(b)}$ - adjusted survivorship curve; * - calculated survivorship, using pooled data on lactating (functional) nipple counts and lactating sows with recent loss of entire litters. Survivorvhip from six months to the first year was calculated using the slope (i.e. the percent of the cohort surviving from the first to the second year) in the crude survivorship curve.

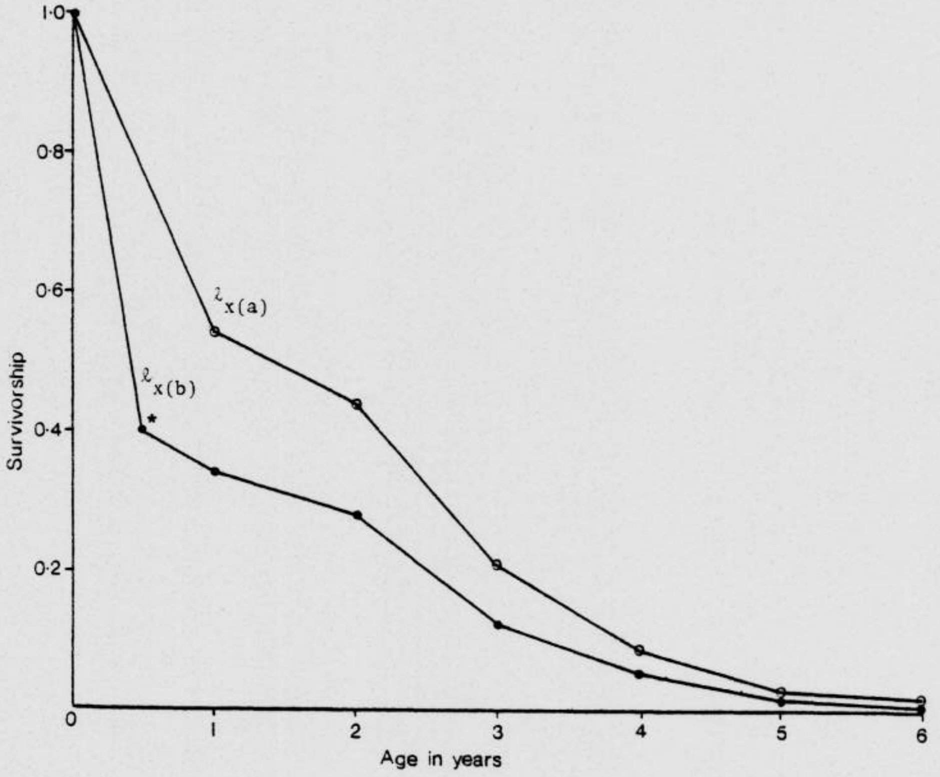

Survivorship
1·0
0·8
0·6
0·4
0·2
0
1
2
3
4
5
6
Age in years
$l_{x(a)}$
$l_{x(b)}$
*

Table 24: Survivorship (ℓ_x) and fecundity (m_x) values for feral pigs in Kipahulu Valley

Age class	Corpora lutea	litter size at birth[1]	litter size at 5 months[2]	ℓ_x	ℓ_x midpoint	I[3]	m_x	$\ell_x m_x$
0-1	4.5	3.5		100	0.40[4]	0.09	0.15	0.06
1-2	7.8	5.8	3.1	34.5	0.31	0.47	1.36	0.42
2-3	8.7	6.8	3.4	28.3	0.20	0.82	2.78	0.55
3-4		5.7	2.8	13.5	0.09	0.65	1.85	0.16
4-5		4.7	3.0	6.1	0.03	(0.65)+	1.52	0.04
5-6		(4.7)+	(3.0)+	2.4	0.01	(0.65)+	(1.52)+	0.01
6-7		(4.7)+	(3.0)+	1.2				
							R_o = 1.24	

[1] estimated from fetal counts

[2] estimated from number of lactating (functional) nipple

[3] incidence of pregnancy

[4] calculated value, see text for details

+ based on preceeding estimate

this carnivore, because of its small size, can effectively handle only juvenile pigs. Accidental crushing, which is the major source of piglet mortality in the domestic pig (Pond & Houpt 1978), cannot be discounted as unimportant in this feral population despite the lack of field evidence. Metastrongyllid and kidney worm parasitism are the most probable direct or indirect causes of adult mortality in their second year. Such an association between nematode parasitism and mortality was observed in a wild boar population in Poland (Fraczak 1974). Failure of dentition appears to be the most likely process limiting the ecological longevity in this population. Thus, if the population turnover is defined as the length of time required for the disappearance of a cohort, then the turnover period in this population (6 years) is less than those published (7-10 years) for populations in Tennessee (Henry & Conley 1978), Poland (Jezierski 1977) and California (Barrett 1971, 1978).

The construction of the adjusted survival curve and its interpretation are dependent on several assumptions. The cohort is assumed to be imaginary because individuals are not born contemporaneously. Differential mortality was not assumed although mortality rates are known to be higher in males than in females in some wild populations (Jezierski 1977; Henry & Conley 1978). Age specific mortality in the recent past is further assumed to be constant. Mortality at six months (60%) may be underestimated. Higher juvenile mortality (70-90%) from birth to six months has been reported in a feral population in California (Barrett 1971, 1978). The interpolation of the calculated survival value at six months to other age intervals using the corresponding percentage mortality in the age-sex composition data overestimates 1_x and is probably an unrealistic approach. Juveniles entering the one-year age class have high mortality during periods when the sow leaves her family grouping for farrowing (Jezierski 1977).

The sample population was derived from three capture methods and these may each have biased its representation to the actual population. The July 1979 to November 1980 trapping program although intensive, probably underrepresented the 0-1 age class (principally pigelts) through trap designs and placement. This bias overestimates 1_x. The incidence of pregnancy is underestimated in some age classes because pregnancy status in trapped gestating sows cannot be definitely ascertained from observations. Thus, the interpretation of mortality patterns or R_o should consider both the shortcomings of the data and biases in 1_x and I, which are most likely over and underestimated, respectively.

(e) Litter size and seasons of birth

Breeding is continuous, but there were more births from November to March and from June to September, suggesting two farrowing periods (Figure 29). The November to March farrowing season coincides with long periods of heavy rains and late winter storms.

The minimum breeding age for sows, estimated by subtracting fetal age from sow's age, was five months. The youngest boar to show spermatozoa in the epididymis was aged at seven months. Based on these

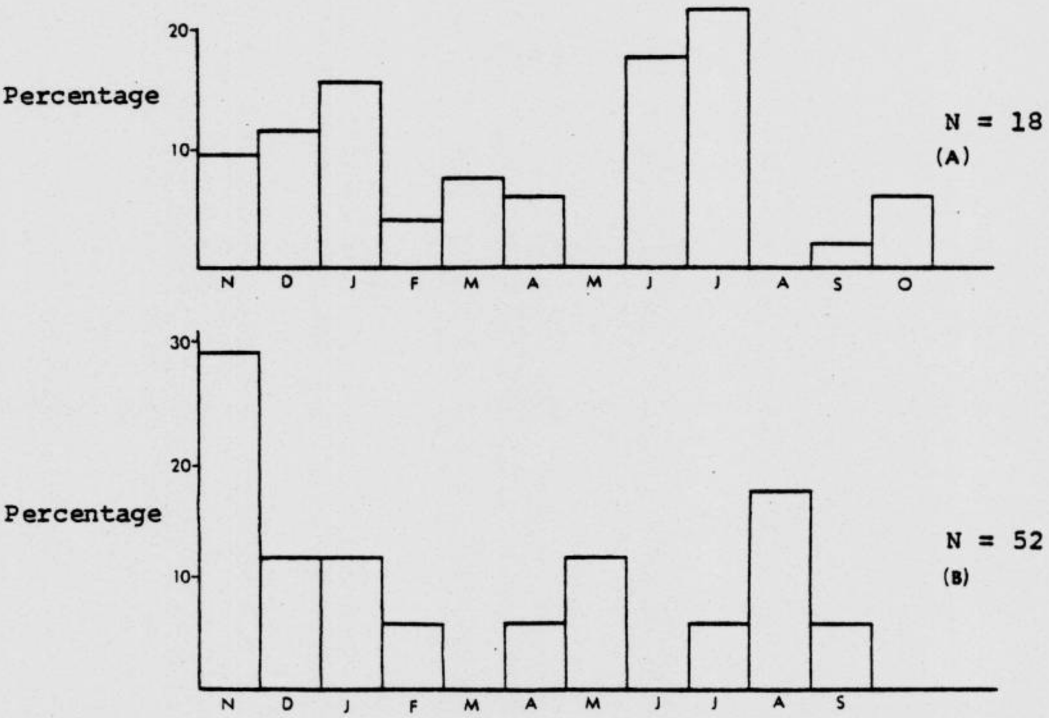


FIGURE 29: Estimated breeding dates of (A) 18 groups of fetuses and (B) 52 trapped animals that were less than one year old.

figures, 41 out of 63 females trapped during the mark-recapture study (July 1979 to March 1980) were sexually mature. Of these, 21.9% were pregnant and 29.3% were lactating. Of the 28 females that were over 5 months, 62.4% (18) were pregnant and 25% (7) were lactating; this proportion included three lactating sows, two of which were one month pregnant and were nursing offspring of only three months. Based on these two observations and a 120-day gestation period published for feral pigs elsewhere (Barrett 1978), the minimum interval between two consecutive litters is 12 months.

The number of fetuses per uterus averaged 5.9 (3-10) in 18 sows (Figure 30). Fetal sex ratio was 56:50 and does not depart from the expected 1:1 sex ratio (X^2=0.34, P>0.50). Mean fetal age was 58.2 ± 21.6 days (N=106). The corpora lutea of pregnancy averaged 7.7 (2-14) in 12 sows whose ages ranged from 7-30 months ($\bar{x}$=19.9). Comparing the mean number of corpora lutea of pregnancy with the mean of the prenatal litter size, the prenatal mortality was, thus, 23.3%.

Total nipple counts in 19 lactating sows averaged 11.1 (8-14); the modal nipple number was 12. The mean number of functional nipples was 3.1, with a range of 1-5 and a mode of 3. Based on the mean values, the ratio of the piglets:nipples was 1:3.7.

Lactating nipples were mostly distributed in the middle (3-4) and posterior (5-6) nipple rows, rather than in the first two rows of anterior nipples. Equating mean number of functional nipples to litter size at weaning (see Methods) and comparing it with prenatal litter

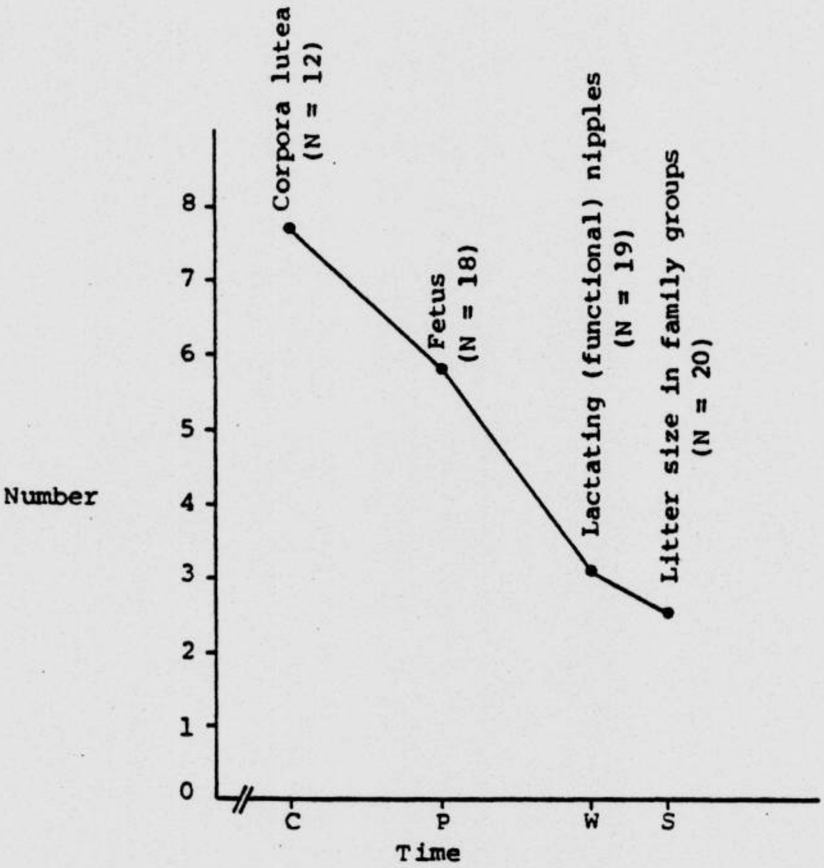


Figure 30: Prenatal and preweaning mortality patterns in feral pigs in Kipahulu Valley. C - conception; P - parturition; W - weaning (4months); S - breeding age (5-6 months).

size, there is thus a postnatal mortality of at least 47.5% to weaning. This is a minimum estimate since observations of lactating sows in the one-animal group type are indicative of loss of whole litters.

Two generalizations on the reproductive biology in domestic and feral pigs can be drawn from published works: (i) pigs are polyestrus, and (ii) high prenatal mortality is characteristic of pigs. Thus, the reproductive success of pigs in the Kipahulu Valley population will be better understood by examining these two extrinsic determinants, mate finding and successful rearing of the young.

Mate finding for feral pigs occupying small home ranges in Kipahulu Valley is less of a problem than in other feral populations in which home ranges cover larger areas. This is because a smaller home range area facilitates increased and more frequent encounters between individuals. This may account for the high pregnancy rate and early breeding age in sows. The lower pregnancy rate in the trapped sample was because early pregnancy status cannot be definitely ascertained by visual inspection. Barrett (1981) described the use of pregnancy detectors to determine pregnancy states in feral pigs without the need of necropsy.

The sow's rearing success, i.e., her ability to wean her full postpartum litter, is low. The data in this study show a prenatal survival of less than 73.3% based on the proportion of corpora lutea represented by fetal count at necropsy, and survival from birth to 5 months of age of 55.3% based on the difference between fetal size and mean number of functional nipples. Thus, the sow loses more than 50% of her offspring prior to weaning. The sources of juvenile mortality have been identified as predation by mongoose, miring in the mud, inadequate weatherproofing of farrowing nests and their susceptibility to flooding, and early evacuation from farrowing nests (Chapter 11). The last two factors are important because piglets cannot effectively thermoregulate during the first two weeks of their postpartum life (Hartsock & Graves 1976).

The estimation of postnatal litter size from counts of functional nipples in lactating sows that was used in this study is well documented (Conley et al. 1972; Diong 1973; Jezierski 1977). Studies in domestic pigs show that piglets initially undergo a nipple sampling and defense behavior, but eventually exhibit nipple specificity by suckling a certain nipple exclusive of all the others throughout lactation (Hartsock & Graves 1976). The observed distribution of functional nipples in the posterior nipple rows rather than in the anterior rows is somewhat puzzling. This is because milk production varies among nipples and is higher in anterior than posterior nipples, and piglets which suckle from anterior teats usually grow faster than those which suckle posterior teats (Wyeth & McBride 1964). Reduced use of anterior nipples in Kipahulu Valley feral pigs may be attributed to the nest bowl structure and nesting materials. Farrowing nests are usually constructed from *Carex alligata* and ferns carefully intertwined and topped over a concave nest bowl. These nesting materials, in particular *Carex*, probably inhibited movements forward to sample for anterior nipple sampling by the feral piglets, and posterior nipples that are first encountered thus become the selected nipples.

The mean number of fetuses per sow in the study ($\bar{x}$=5.9) is lower than those reported by Giffin (1978) ($\bar{x}$=6.4) for another rain forest habitat, Pavlov (1980) for the feral population in Australia ($\bar{x}$=6.7) and Sweeney et al. (1979) for a feral population in South Carolina ($\bar{x}$=7.4), but comparable to that in California (Barrett 1971) ($\bar{x}$=5.6). These differences could in part be the result of age and weight differences which are known to affect fecundity. A reasonable alternative hypothesis is that small home ranges in a topographically isolated area will encourage inbreeding tendencies in this feral population and result in lower reproductive performance. According to Anderson (1974), inbreeding in feral pigs produces negative effects on litter size by lowering ovulation rates. This genetic factor may be the cause for the lower fecundity in this population.

High piglet mortality in the Kipahulu population is probably inconsequential to the maintenance of this feral population because feral pigs breed all year round and do not appear to be energy or protein limited. Using the age-sex data described earlier, it can be seen that a sow in her life-time, despite a postnatal mortality of 45%, will potentially be able to maximally replace herself with at least 16 sows over 11 farrowing occasions.

(f) Group size composition and behavior

Four group types were identified. Solitary animals were usually boars older than one year, but sometimes were yearlings, lactating sows or stray piglets. The family group consisted of a sow and her offspring of the season, while the extended family group was made up of a sow and her offspring from the current and previous season. The mixed-group was comprised of subadult and adult animals, with or without juveniles. Among group types, the family unit was most common (Figure 31).

Overall mean group size averaged 2.62 ± 1.65 and ranged from 1 to 9 animals in 58 groups, totalling 161 pigs (Figure 31). When the one-animal group size was excluded from the calculations, overall mean group size averaged 3.64 ± 1.52 animals. Mean group size in koa forest ($\bar{x}$=2.98, N=48) was larger than in ohia forest ($\bar{x}$=1.8, N=10). The modal group size was one. Group size of three was the second most common in the size frequency distribution. Groups larger than six animals were rarely seen. The largest group size was nine, and comprised of two sows and their litters.

Using all sighting records on family units during the study period, two size fluctuation peculiarities were observed in sow-offspring associations: (i) a marked reduction in family group size from 4.64 ± 0.72 (N=14) when piglets were 1-2 months, to 3.45 ± 0.86 (N=20) when piglets were between 2-6 months old. This observation indicates a preweaning mortality of at least 32.7% from 1-6 months, and (ii) a change in group composition resulting from boar entry when piglets were

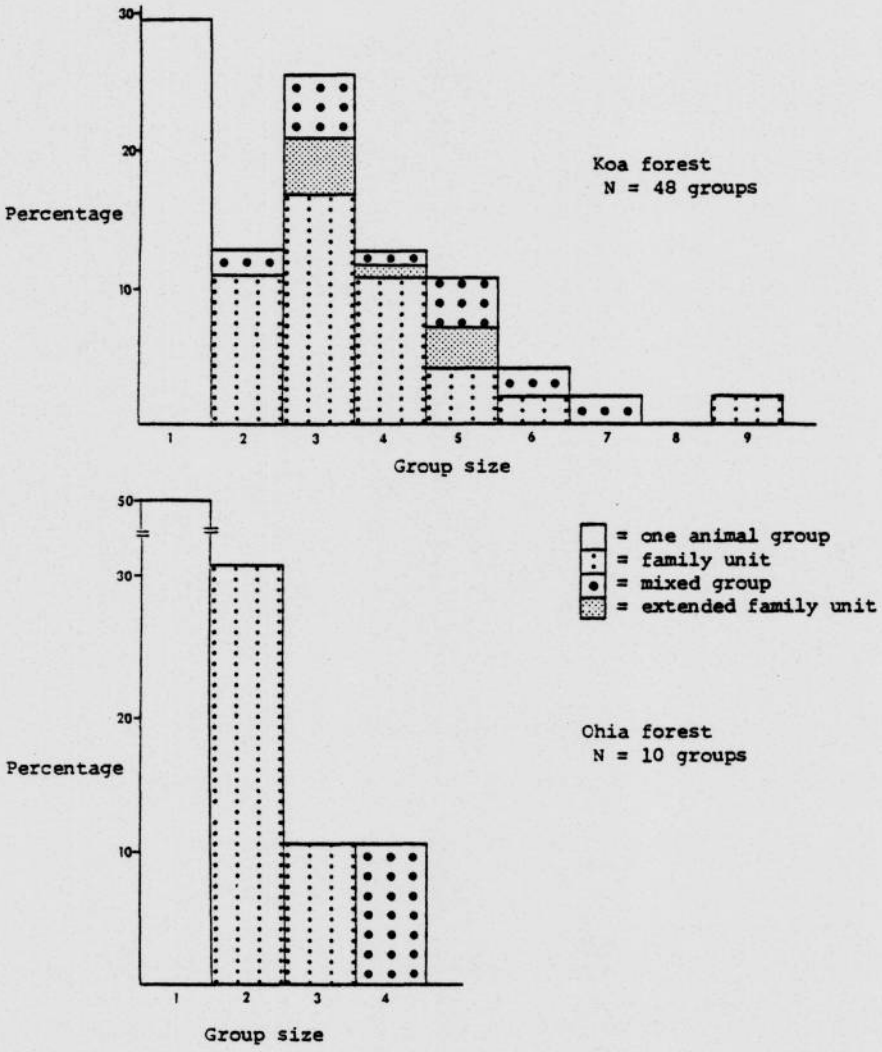


FIGURE 31: Group size and group type frequency distribution in feral pigs from koa and ohia forests in Kipahulu Valley.

as young as 2 months. The family unit can last for as long as 8 or more months. This conclusion is drawn from necropsy observations on a few lactating sows which were already pregnant when the offspring were between 3-4 months.

Group behavior showed several unique characteristics. The most outstanding was the close proximity among group members whenever a group was seen engaged in foraging, resting or locomotory activities. Groups normally fed together and concentrated their rooting activities within a common foraging area before moving on to another site. Boars in mixed-group units containing an estrus sow were observed on two occasions to perform two peculiar behaviors: (i) slashing bases of tree trunks with their canines and subsequently marking them with large amounts of foamy saliva, and (ii) jaw-champing, during which time the snout was directed upward, the air was sniffed and the jaws were repeatedly snapped. Whenever human presence was first sensed, members in a group generally remained still momentarily, maintained fixed gazes in the direction of the humans and usually vocalized before moving away. Whenever a group was frightened, flight was usually initiated by one group member with the remaining members following. The opposite of this group behavior and cohesiveness was regularly seen in the trapline. When one or two members of a family or an extended family group was trapped, the remaining untrapped group members camped at the trap site. Flight behavior in the sow-offspring units differed from other group types in that nursing sows normally move away first and ahead of her offspring. In family units with offspring less than 2 months, the juveniles respond to gunfire or human presence by temporarily crouching on their legs among the ground vegetation, rather than attempt to catch up with the fleeing mother, and then later running away. Flight distance, defined here as the minimum distance an animal could be observed or approached before onset of flight, was recorded as 2m. Flight distance was generally smaller for mixed groups but larger in sow-juvenile group types.

Two generalizations can be made on grouping patterns in the feral pig. The first is that all group types are breeding units. The most frequent sightings were of single pigs and this is also the case with other feral (Barrett 1971; Pavlov 1980) and wild populations (Singer 1977; Shaffer 1979). The second generalization is that all group types are derived from family units. Boars leave the family unit at about 9 to 12 months for a solitary life, and rejoin a group only for breeding opportunities (Barrett 1971). Field sightings of boars in family units of lactating sows indicated regrouping of solitary boars with a family unit for breeding opportunities. Enlargements of the family unit into other group types was clearly evident from field observations; this process was observed extensively in a feral population in California (Barrett 1971). Thus, the family unit is the basis of social structure in feral pigs.

Mean group size of feral pigs in Kipahulu Valley is smaller than those reported by Signoret et al. (1968) ($\bar{x}$=8, range of 1-80), Barrett (1971) ($\bar{x}$=8.4, range of 2-97) and Pavlov (1980) ($\bar{x}$=7.6, range of 1-17) for other feral populations. The absence of groups larger than nine and the lower mean group size in this population, may be due to the relative difficulty of movement for large groups in this broken and dense rain forest.

Alternatively, the smaller average group size observed in this study may be a function of the number of surviving offspring at six months; high reproductive success will favor the formation of larger group types. As was observed earlier the reduction in family unit group size during lactation indicates a piglet postnatal mortality of 32.5%. This estimate is a minimum because of observations of lactating sows without any accompanying offspring thus suggesting probable loss of entire litters. The lower group size in ohia forests was apparently the result of a lower reproductive success due to limitation in the number of adequate shelters. Whereas farrowing nests (N=2) in the koa forest were built in tree holes and caves, those in the ohia forest (N=7) were constructed on open, unsheltered grounds. These nests were not weatherproof and were prone to flooding. This most likely explains the higher piglet mortality and the smaller group size.

The group behavior reported here and the reactions of these pigs to humans may be accounted for by examining the sensory functions in feral pigs. Sense of sight in pigs is poorer than that of smell and hearing. Their ability to focus has been questioned. Acoustic signals are thus of major importance in inter-animal attachment, group cohesion and organization of social behavior. More than 20 sound types of social importance have been identified (Signoret et al. 1968). Pheromones also serve to regulate group behaviors. The stability of the family unit, for instance, is maintained by a pheromone produced by the mammary gland; this pheromone bond serves to attract and encourage attachment of young to the mother (Hafez & Signoret 1969). The submaxillary and preputial glands in adult boars produce the sexual pheromone, delta-16-androstene (Sink 1967; Pond & Houpt 1978), which serves to attract estrus sows and mediate the boar's rejoining with a group.

CHAPTER 9

HOME RANGE, MOVEMENT AND ACTIVITY PATTERNS

Introduction

The home range and movement patterns of the feral pig are of major importance in any management program. Such studies on wild and feral populations in other areas have yielded information on habitat preferences, home range traditions and a better understanding of life history strategy in this animal (Barrett 1971, 1978; Kurz & Marchinton 1972; Giles 1978; Wood & Brenneman 1980). This information has in turn assisted biologists to predict the pig's influence on a given ecosystem and made it possible for managers to plan control programs. Size of pig's home range in a given habitat must be taken into consideration when planning a control program (Tester & Siniff 1974).

Home range determinations necessitate the collection of data on the consecutive locations of tagged animals. In early studies on home ranges of the pig, a single interrupted or continuous mark-recapture program was normally used to collect locational data. Capture-recapture data are usually influenced by bait, trap variables (Chapter 8) and animal behavior. Direct sighting is the simplest, sometimes preferred, method of collecting data (Jewell 1966) and this technique has been used to describe home ranges of feral pigs in the Sierra foothills, California (Barrett 1971, 1978). The dense forest vegetation and restricted human mobility in the Valley precluded use of follow-the-animal method or tag-resight data for recording home range.

Radioactive substances have been used to obtain animal locations, but rapid fecal deterioration in the rain forest and other habitat considerations make this study method undesirable. Radio-tagging with transmitters has the potential of establishing a continuous data-link between an investigator and study animals whose locations can be recorded at a distance.

Radiotelemetry was used to collect location data. This method has been used effectively in home range and movement studies for many other terrestrial vertebrates (Werber 1970; Will & Patrick 1972) but only to a limited extent for wild and feral pigs, and two other pigs (Table 25). The enclosed nature of the Valley would allow effective use of radiotelemetry for addressing questions on the pig's movements and home ranges. Theoretically, radiotracking is more efficient in providing a greater number of locational data per unit effort than sighting or trapping (Lance & Watson 1979). Moreover, such data are relatively free of biases inherent in other methods of studying home ranges (Mech 1974). Habitat impact resulting from research activities would be minimal compared to the other methods of data collection mentioned above.

At the outset of this phase of the study, it was decided that information on the locations of the pigs will be more important than their activities for its management. Thus, the main objectives of this study were to delineate and determine home range size and to describe movement patterns of pigs in the Valley.

TABLE 25: Examples of home range and movement studies in free-ranging pigs using radiotelemetry.

Location	Radiotagged animals			Reference
	Population	N	Transmitter frequency (MHz)	
United States				
SRP[1], South Carolina	feral pig†	15	150	Wood and Brenneman (1980)
Hobcaw Barony, South Carolina	feral pig†	7	27	Kurz and Marchinton (1972)
GSMNP[2], Tennessee	European wild boar†	13	161	Singer et al. (1981)
TWMA[3], Tennessee	European wild boar†		27	Conley et al. (1972)
Australia				
Girilambone, New South Wales	feral pig†	3	60	Pavlov (1980)
France				
Chize Forest	European wild boar†	4	72	Mauget and Sempere (1978)
Chize Forest	European wild boar†	8	72	Mauget (1979)
Gresigne Forest	European wild boar†	1	148	Spitz and Janeau (1979-per.comm.)
India				
Barnadi Forest Reserve, Assam	Pigmy hog††	2	150	Oliver (1979)
Africa				
Sengwa Research Area, Rhodesia	Warthog†††	8	48	Cumming (undated)

† *Sus scrofa*
†† *Sus (Porcula) salvanius*
††† *Phacochoerus aethiopicus*

[1] Savannah River Plant
[2] Great Smoky Mountains National Park
[3] Tellico Wildlife Management Area, Tennessee

Materials and Methods

(a) Transmitters

Transmitters (Wildlife Materials, Inc., Illinois) were powered with a 3-volt, 20,000 mah lithium battery and operated in the 160-161MHz frequency range. Each transmitter broadcast on a different frequency so that tagged animals were distinguishable. Six of the 12 transmitters had the activity, mortality and steady pulse transmission modes; the others had the steady pulse transmission mode only. Activity monitors threw in an extra pulse when the animal was active. The mortality transmission mode, 3-4 times faster than the steady pulse, would be activated only after the transmitter was perfectly stationary for six hours, as would be the case when the collar was removed from the animal or when the animal was dead.

(b) Collar attachment

Pigs were captured in corral and box traps baited with shelled corn or coconut. Captured animals were immobilized or manually restrained, eartagged, weighed, sexed and aged by their dentition. Manually restrained animals were hung upside down from a tree for collar attachment. This restraining procedure, suggested by Dr. R. H. Barrett, University of California, Berkeley, proved most convenient for collar attachment. Delgado's (1963) "rule of the thumb" was applied to ensure a snug collar attachment. Collars were secured in position by locking the overlapped free ends with steel pop rivets. Instrumented animals were then returned into the trap for 1 to 2 hours for observations on collar acceptance before their release.

(c) Monitoring methods

Directions were determined from fixed site antenna stations but principally from ground-tracking using a hand-held 2-element Yagi antenna (Telonics, Arizona) or a collapsible 3-element Yagi and a Falcon Five receiver (Wildlife Materials Inc., Illinois). The receiving system at each fixed-site station consisted of a two 10 element Yagi array, arranged in a null-peak phase, and elevated 3 or 10m above the ground. Directions of ground-tracked animals were determined by their signal maxima, while those determined from fixed-site stations were by the null-peak mode. At each reading location, the hand-held antenna was swept around 360 degrees for each frequency. If radio contact was established or if direction finding was possible, the sweeping was gradually reduced in the direction of the loudest signal at a set receiver gain. Regardless of mode of direction finding mentioned above, the receiver gain was lowered until the signal just disappeared or was just audible. The bearing from which the just-audible signal was heard was recorded as the direction for the tuned-in animal. Total reading time varied from 1-4 minutes; the time interval between reading locations varied from 15-30 minutes.

From November 1979 to March 1980, diel locations of five animals were simultaneously monitored from two fixed-site stations, at 3-hourly intervals by two investigators who were in radio contact. An animal was recorded as active when the activity monitor was activated for more than 50% of the time during the tuned-in period.

(d) Data analyses

Locations were plotted by triangulation on U.S. Geological Survey Maps on a scale of 1:8000. Bearings which intersect acutely at less than 20 degrees or obtusely at greater than 150 degrees were rejected for plotting. Locations were transferred to an X-Y coordinate-type grid overlay for home range delineation and calculations of the geometric center for the entire and seasonal home ranges, following Hayne (1949).

Several estimators of home range area have been developed mostly for territorial mammals and of these, three have been previously used to describe home ranges of free-ranging pigs (Table 26). For this study, home range size was calculated by the minimum-area method (Mohr 1947), modified minimum-area method (Harvey & Barbour 1965), standard diameter (Calhoun & Casby 1958) and the elliptical covariance matrix determinant model (Jenrich & Turner 1969). The standard diameter measure, unlike the elliptical model, assumes circular distribution of locational data. The distribution of animals' locations were thus tested for circularity using eigenvalues (Sokal & Rohlf 1969). Home ranges and diel ranges delineated by the minimum-area methods were measured for their areas using a compensating planimeter and described further by the following linear measurements: range length major axis, range length minor axis and range length-width ratio (Kurz & Marchinton 1972).

TABLE 26: A summary of commonly used methods for calculation of home range size.

Home range estimators	Species	References
Minimum area method (convex polygon)*†	Rabbits, armadillo, small mammals	Mohr (1947)
Modified convex polygon (minimum polygon)*†	Voles	Harvey & Barbour (1965)
Inclusive boundary strip	Artificial population; mice	Blair (1940); Stickel (1946, 1954)
Exclusive boundary strip	Mice	Stickel (1946, 1954)
Added squares	Mice	Manville (1949)
Observed range length	Artificial population	Stickel (1946, 1954)
Adjusted range length*	Artificial population, mice, vole	Stickel (1946,1954); Hayne (1949)
Standard circle (recapture radii)*†	Rats, mice, squirrels	Harrison (1958); Calhoun & Casby (1958)
Koeppl's bivariate model	Ground squirrel	Koeppl et al. (1975)
Size index	Artificial population; mice	Metzgar & Sheldon (1974)
Elliptical approximation	Coyote	Gipson & Sealander (1972)
Covariance determinant model†	Rabbit, lizzard	Jenrich & Turner (1969)
Quartile deviation measure	Bullfrogs	Van Winkle et al. (1972)
Harmonic mean of aerial distribution	Rabbit	Dixon & Chapman (1980)

* Methods that have been used in estimating home ranges of wild and feral pigs.

† Estimators used in this study.

Movement patterns were further described using mark-recapture results (Chapter 8), the 24-hour monitorings, and field observations. Diel home ranges were computed as the minimum total distance moved in a diel period (MTD).

Results

(a) Effect of radiotagging on study animals

The neck collar did not appear to produce discomfort on head or body movements. Regardless, tagged pigs made vigorous attempts to remove the collar by rubbing their necks against the sides of traps, but appeared to accept the collar after 1-2 hours. Total weight of the collar-transmitter was much less than 5% of body weight (Table 27), the weight load limit generally observed by most workers. Boar 650 recaptured 2 months later at E6 and sow 450 shot by a hunter, had neck abrasions and hair loss, but no apparent weight loss. Movements of tagged animals during the study duration were unlikely to have been influenced by the collar transmitter.

(b) Home range size and configuration

A total of 934 animal locations were recorded from 13 adult pigs monitored for periods ranging from 1-17 months. Home range size was delineated and estimated for five boars and four sows monitored for more than 3 months (Figure 32). Home range size varied greatly among the four estimators (Table 28). The modified minimum-area method gave the smallest area, while the standard diameter model gave an inflationary

TABLE 27: Biological data, length of radiotracking period and number of radiolocations for 13 feral pigs in Kipahulu Valley.

Instrumented animals					Weight of Radiocollar (g)	Length of study		Radiolocation (total)
Identification	Age (months)	Weight (kg)	Sex	Release Site		Tracking period	Total Months	
197	20	68*	♀	E 1	465	7. 7.79- 4.15.80	10	132
244	9	54	♂	E 9	458	5.26.79- 4.15.80	11	116
290	8	36*	♀	E 2	460	8.18.79- 1.20.80	5	42
350A†°	7	27*	♀	K 1	459	2.18.79- 3. 9.79	1	28
350B	14	59*	♀	E11	459	2.25.80- 4. 8.80	2	12
394	12	40	♂	E10	455	9.15.79-10.30.80	13	111
450‡°	8	29*	♀	K 1	458	2.18.79- 9.24.79	7	9
550	11	50*	♀	L 2	454	8.17.79- 1.27.80	6	76
600	8	38	♂	E12	459	8.10.79-12.14.80	14	87
650	13	57	♂	E 6	464	7.21.79-12.14.80	17	148
700	9	45*	♀	E 8	463	7.21.79- 9.30.80	14	124
800°	8	31	♂	K 1	455	2.18.79- 2.10.79 7.17.79- 1.25.80	6	25
850	22	63	♂	E 8	453	7.21.79-10.26.79	3	24

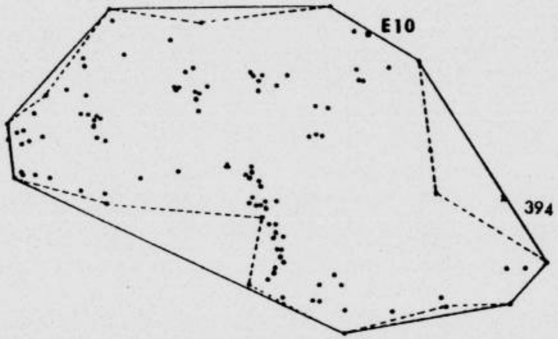
† extricated collar recovered and reused on 350B

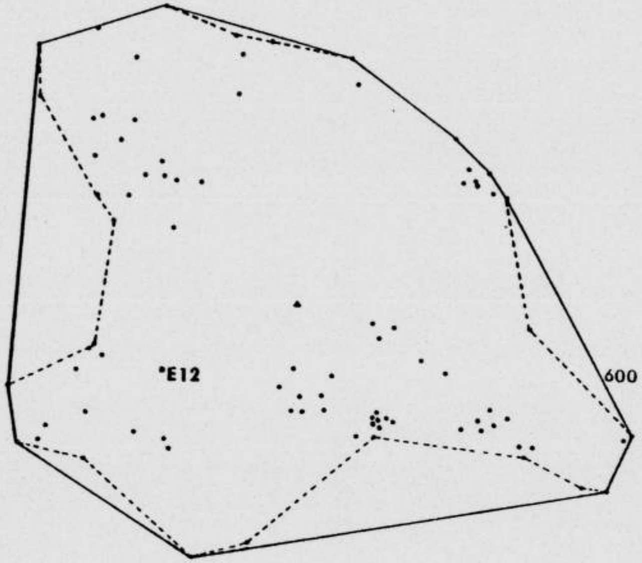
‡ shot by a hunter

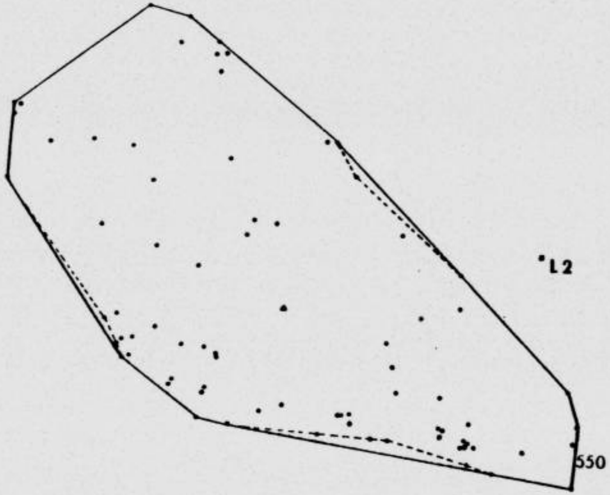
* estimated from chest measurements

° collar and chest harness, all other pigs instrumented with collars only

Figure 32: Home ranges of nine feral pigs delineated by the minimum-area (solid lines) and modified minimum-area (broken lines) methods. Alphanumerals - release site; 3-digit numbers - tagged animals; ▲ - geometric center of home range.


E10
394


E12
600


L2
550

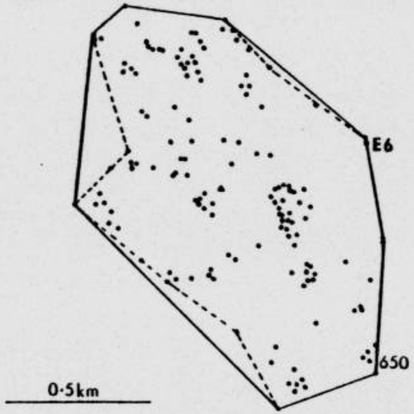

E6
650
0·5km

TABLE 28: Home range size estimates for nine feral pigs in Kipahulu Valley.

Animal identification number	Length of study (months)	Home range size (km^2)			
		Minimum-area	Modified minimum-area	Circular measure	Elliptical measure
Boars					
244	11	2.13	1.61	13.88	5.32
394	13	1.48	1.20	7.95	2.36
650	17	1.59	1.53	23.36	1.42
600	14	2.90	2.41	17.16	5.56
850	3	0.79	0.74	6.86	2.08
Mean[1]	11.6	2.03	1.68	15.58	3.67
Sows					
197	10	0.65	0.63	3.21	0.90
290	5	0.87	0.77	2.96	0.77
550	6	1.73	1.70	13.82	3.88
700	14	1.22	1.14	6.43	1.94
Mean	8.7	1.12	1.06	6.61	1.87
Overall mean[1]	10.3	1.57	1.37	11.09	2.77

[1] Based on animals monitored for more than five months.

estimate. Based on the premise that the minimum area (convex-polygon) will approach the actual home range size as the number of animal locations are increased, then the modified minimum-area was 12% too small and the circular and elliptical measure, 615% and 78% too large, respectively.

With the minimum area estimator, the home range size for eight pigs monitored for more than 5 months ranged from 0.65 to 2.9km^2 and averaged 1.57 ± 0.67km^2. Mean home range size for four boars (2.03 ± 0.56km^2) was significantly larger ($t=2.83$, $P<0.05$) than the mean home range size (1.12 ± 0.41km^2) for four sows. Home ranges of two boars in the ohia forest were larger than for two other boars in the koa forest. The home range of one sow in the ohia forest was larger than those for three sows in the koa forest. There was extensive overlap in the pigs' home ranges (Figure 33) and in seasonal home ranges, but with little seasonal shifts in the geometric centers. Summer and winter home ranges were not different in four animals monitored for one calendar year.

Home ranges were irregular in their configurations. Circularity tests showed that the distribution of animal locations for all study animals was non-circular, as indicated by the ratio of the eigenvalues (Table 29). The home range of one animal (600) approximated a circular configuration. Home ranges were longer than wide (Table 30). Two sows had home ranges whose range lengths were more than twice the range widths. Average range length axes were longer ($P>0.20$) for boars than for sows. Range length:width axis ratio did not differ between sexes ($U=4$, $P>0.20$). The spatial distance of locations (Figure 32), the

Figure 33: Composite home range maps of nine feral pigs in Kipahulu Valley , Maui. Home ranges are delineated by the minimum-area method. Note the extensive overlap in the home ranges. Three-digit numbers denote radiotagged pigs; solid lines - home ranges of boars; line screen - home ranges of sows.

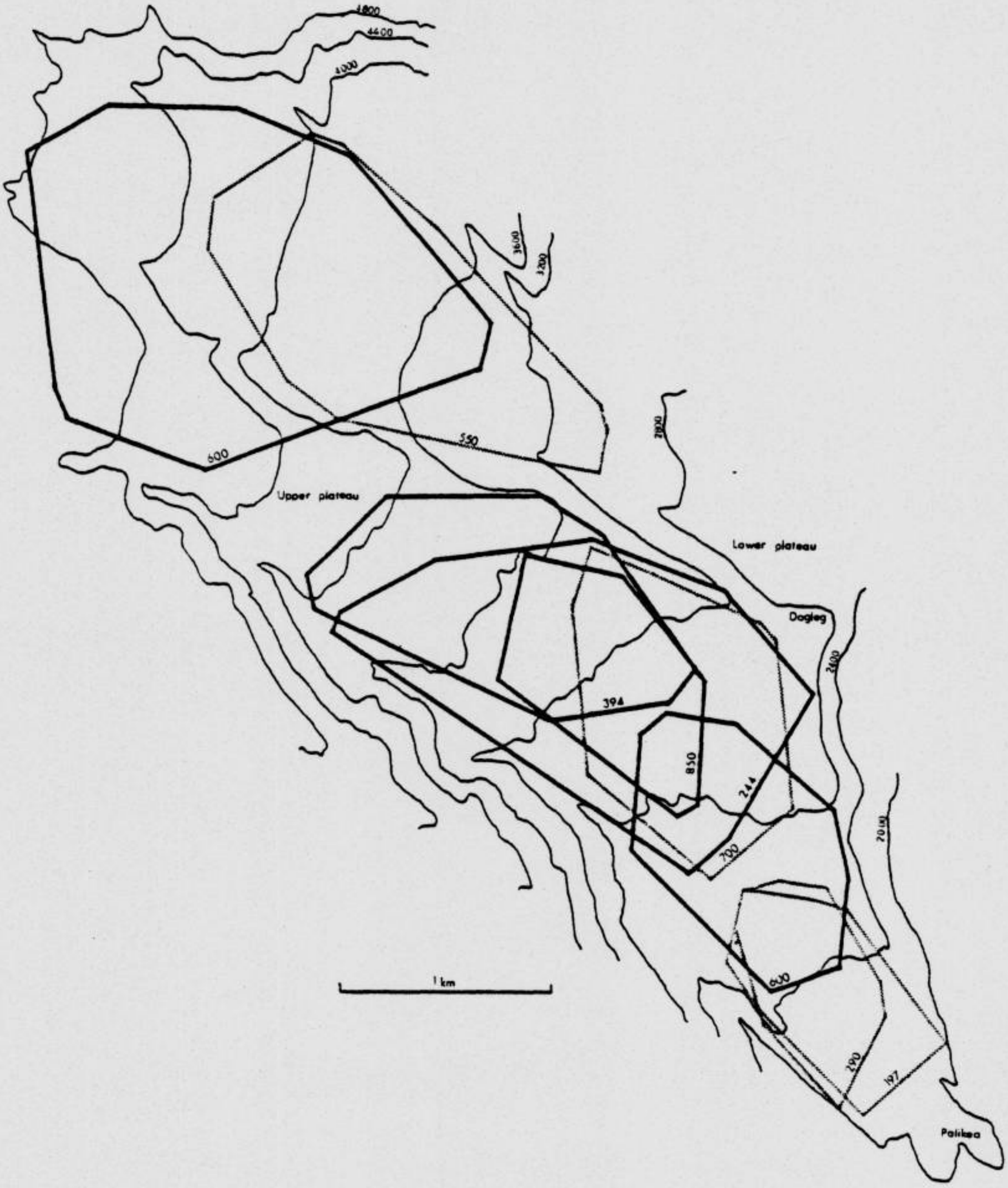

4800
4400
4000
3600
3200
2800
600
550
Upper plateau
Lower plateau
Dogleg
2400
394
850
244
700
2000
600
1 km
290
197
Palikea

TABLE 29: Results of circularity test for home ranges of 9 feral pigs in Kipahulu Valley. A home range was considered to have a circular conformation when the ratio of the eigenvalues ($\frac{\lambda_1}{\lambda_2}$) approaches one.

Animal identification number	λ_1	λ_2	$\frac{\lambda_1}{\lambda_2}$
197	299.65	116.79	2.56
244	947.08	220.76	4.29
290	183.14	48.54	3.77
394	519.90	137.28	3.78
550	889.72	233.12	3.81
600	2397.39	1839.44	1.30
650	347.52	83.13	4.18
700	389.90	136.19	2.86
850	383.83	151.83	2.52

TABLE 30: Home range axis lengths for eight feral pigs in Kipahulu Valley

Animal identification number	Range major axis[1] (km)	Range minor axis[2] (km)	Range major : minor axis ratio
Boars			
244	2.35	1.25	1.88
394	1.93	0.98	1.96
650	1.50	1.13	1.32
600	2.45	1.66	1.47
Mean	2.05	1.25	1.65
Sows			
197	1.25	0.68	1.83
290	1.21	0.60	2.01
550	2.35	1.04	2.25
700	1.75	1.04	1.68
Mean	1.64	0.84	1.94
Overall mean	1.85	1.04	1.77

[1] Distance between extreme radiolocations.

[2] Perpendicular distance along the major axis at the widest point of the minimum home range.

ratios of the eigenvalues (3.23 ± 0.93) and the range length and width axes (1.77 ± 0.28) show that home ranges of feral pigs were elongated in shape.

Home ranges of six pigs on the upper plateau were bordered by the central escarpment and the Koukouai Gulch, while the home ranges of three other animals were bordered only by the central escarpment ridge (Figure 33). The center of activity (geometric center) for all pigs monitored on the upper plateau were sited away from the plateau's long ridge crest; the mean least distance of the centers of activity from the central escarpment for upper plateau home ranges was 0.56 (0.43-0.7) km. Animals 394 and 550 had their activity centers on the lower plateau near the bottom of the central escarpment.

(c) Movement and activity patterns

(i) Daily movements and activity patterns.—Diel home range size of boars was two times larger than that of sows and varied from 0.06 to 0.28km for both sexes (Table 31). The range major:minor axis ratio was similar for boars and sows and averaged 2.46 ± 0.34km in six animals. Mean total distance travelled during a 24-hour period was, however, greater ($U=5$, $P<0.10$) in boars (1.17 ± 0.24km) than in sows (0.74 ± 0.11km). Diel movement patterns were mostly linear and clustered. During a 24-hour period, pigs showed a tendency to move out from their night resting sites during early morning and return to their resting sites along similar paths in the late afternoon. Diel monitoring that coincided with periods of heavy rainstorms in December and February

TABLE 31: Diel home range parameters for 3 boars and 3 sows monitored from November 1979 to March 1980 in Kipahulu Valley.

Animal identification number	Number of 24-hour tracking periods	Number of locations	Diel range size (km^2)		Diel range major axis		Diel range minor axis		Diel major : minor axis range		MTD	
			$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
Boars												
244	9	70	0.28	0.15-0.39	0.57	0.39-0.72	0.28	0.17-0.40	1.97	1.25-3.54	1.46	0.95-2.00
394	5	38	0.24	0.18-0.32	0.51	0.41-0.62	0.23	0.10-0.30	2.20	1.48-4.50	1.20	0.94-1.41
650	9	68	0.09	0.03-0.15	0.34	0.17-0.43	0.15	0.10-0.24	2.26	1.26-4.30	0.86	0.45-1.00
Sows												
197	8	55	0.06	0.02-0.13	0.28	0.21-0.39	0.10	0.05-0.17	2.82	1.42-6.01	0.60	0.40-0.83
290	5	40	0.13	0.05-0.13	0.36	0.11-0.21	0.14	0.11-0.21	2.57	1.74-3.86	0.88	0.62-1.04
700	8	61	0.08	0.05-0.13	0.35	0.20-0.54	0.12	0.08-0.21	2.91	1.22-5.40	0.73	0.62-1.04

Mean total distance (km).

showed that pigs tended to restrict their movements to the vicinity of a shelter site and to shelter overnight away from their normal night shelters. There was less linear movement from 2100-0300 hours and from 1200-1500 hours than during other periods of the day, suggesting night and day resting periods between foraging activites. Signal activity patterns from four pigs showed biphasic diel activity cycle with high activity periods in early morning and late afternoon (Figure 34).

(ii) Movements into and out of the Valley.—One of the objectives of the tracking study was to determine if there were movements in and out of the Valley. Signal extinction was used to establish such movements. Whenever radio contact with a tagged animal was broken, ground tracking was conducted from Kaumakani Ridge, Lower Kipahulu or in the Cable ridge area in an attempt to relocate the animal.

Lateral exit movements from the west side of the lower section of the upper plateau into Koukouai Gulch was established for two pigs (Figure 35). On February 18, 1979, a group of three pigs captured in a corral trap at K1 were instrumented with radiocollars. The pigs stayed overnight in a koa tree tunnel 30m from K1. On March 9th, the frequencies of the three animals were tuned in from the Palikea fixed site station. A mortality signal from 350A was received, but not the transmissions from the other two pigs. Subsequent ground tracking along Koukouai Trail located the collar of 350A at C1 (Figure 35), 250m downslope from the release site and sow 450 in Koukouai Gulch. Animal 450 remained in the Gulch from February to September, when a mortality signal was received from C2. The fate of this animal was known only in

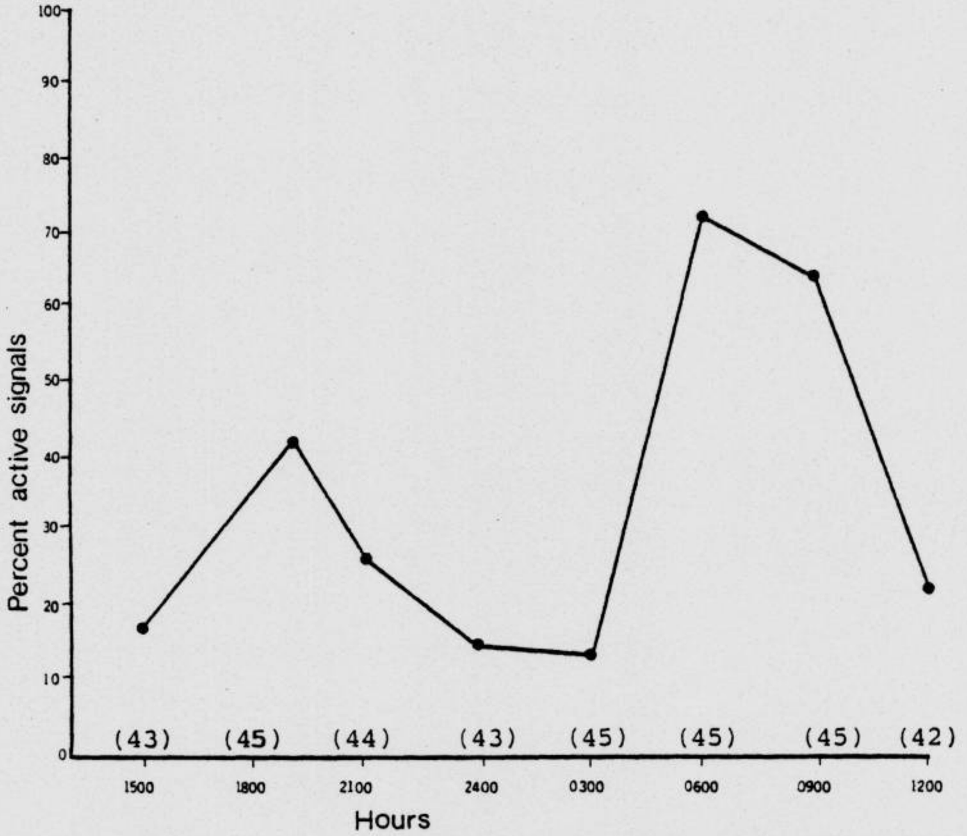
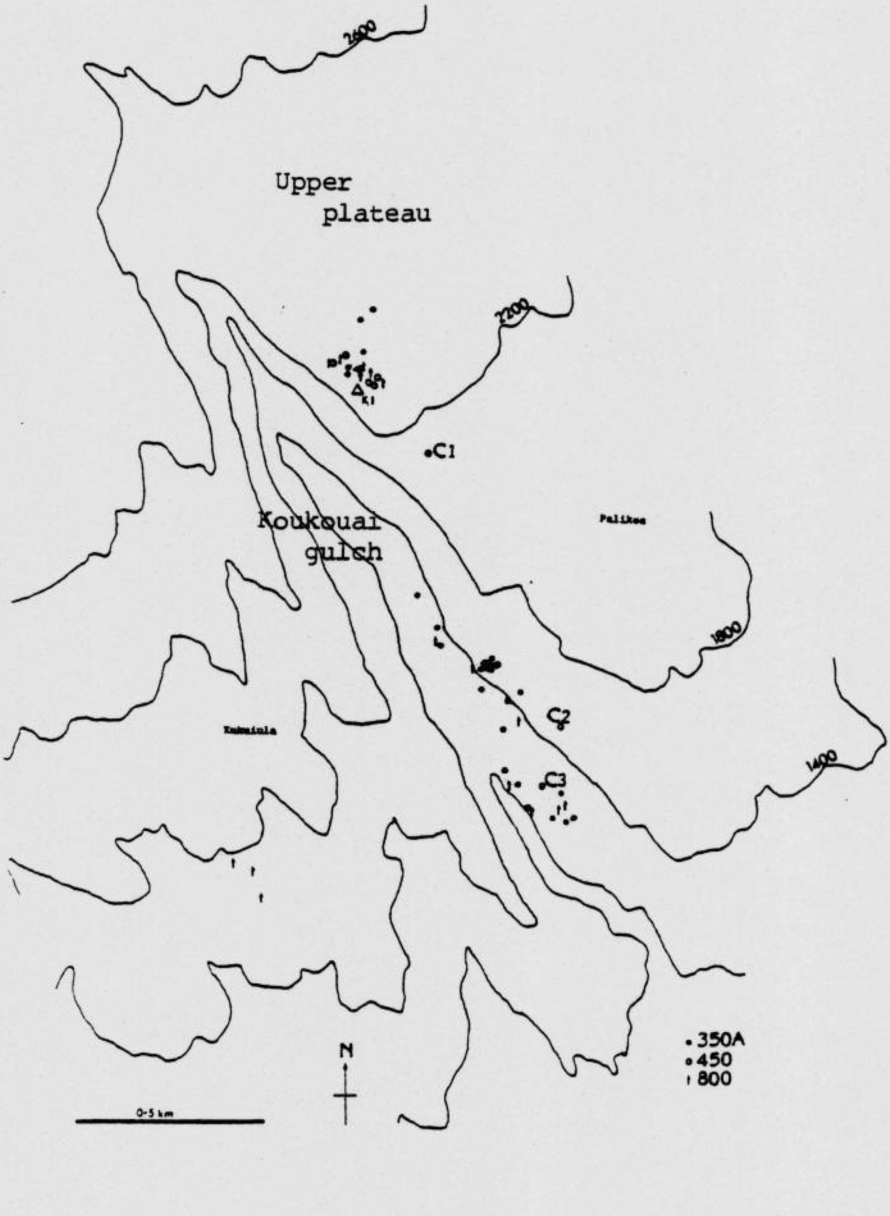


Figure 34: Diel activity cycle of five feral pigs monitored from November 1979 to March 1980. Parenthesized values indicate total number of three-hourly signal readings. Note the biphasic activity pattern.

Figure 35: Locations and entry-exit movement patterns of three radiotagged feral pigs in the lower section of the upper plateau, Kipahulu Valley, Maui. Animal locations in the Koukouai gulch are determined from large error polygon formed by bearings with ± 5 accuracy. C1 - collar of animal 350A; C2 - location of collar 450; as determined from groundtracking; C3 - location of collar as determined by a Park ranger; K1 - corral trap.


2600
Upper
plateau
2200
K1
C1
Koukouai
gulch
Palikea
1800
C2
C3
1400
N
0-5 km
350A
450
800

January 1980 when a hunter admitted to shooting the pig during a dog-hunt in the Gulch. Boar 800 could not be located in the Gulch and transmitter failure was assumed. On July 17th, 1979, radio contact with 800 was reestablished from Kaumakani Ridge. A day's groundtracking on Cable Ridge located the animal in Kuikuila. Boar 800 returned to Koukouai Gulch sometime in November, and remained there from December 1979 to January 1980. The probable movement routes for 350A, 450 and 800 are as shown in Figure 35.

(iii) Barriers to movement.—Trap-revealed movement patterns (Chapter 8), tracking studies and field observations, collectively show that some sections of the central escarpment do not present a physical barrier to intervalley pig movements. In the upper sections of the Valley the home range of boar 600 straddled both plateaus. Boar 600, captured in E12, remained in this vicinity on the upper plateau from September to December 1979, but ranged in the lower plateau for the rest of the tracking period. Its activity center was sited in the lower plateau near the base of the central escarpment. Interplateau movements probably took place between E1540-E1600m. In the lower section of the Valley, lateral movements between plateaus near Palikea were established from mark-recapture studies (Chapter 8). Pig trails from the interior of the upper plateau that arrived at the central escarpment usually followed the escarpment research trail upslope or downslope and for no more than one kilometer trail length before deflecting into the plateau again. Occasionally, pigs would forage or shelter overnight under overhanging cliffs up to 60m down the escarpment slope before returning to the interior of the upper plateau for lateral movements to rooting sites near the central escarpment.

Fallen trees were also observed to deflect movements. Pigs preferred to crawl through gaps between tree logs and the ground, or trail along the length of a fallen tree than to jump over it. Deeply undercut streams, stream swelling and localized flooding during winter months are likely barriers to movements.

Discussion

Home range is a well-understood biological concept, however, a plethora of methods (Table 26) exist for the estimation of home range size and the estimates from different methods can vary. Methods which are mathematically complex need not necessarily give greater biological insight (MacDonald et al. 1979). Of the four area estimates used in this study, two (circular and elliptical measure) assume a bivariate distribution while the other two (minimum-area and modified minimum-area) do not make assumptions about distributions. Methods for testing locational data for confirmation to bivariate distributions are not available, except for the circular measure of Calhoun and Casby (1958). The circular measure gave an inflated, unrealistic area which extends outside the Valley and includes grounds not covered by the pig. Circular normal estimates of home range are larger than a bivariate estimate (MacDonald et al. 1979). The circular model of Calhoun and Casby depends on sample size and assumes an equal probability of locating an animal within a circular area; this restrictive assumption has been termed a "historical accident" (Jenrich & Turner 1969). Circularity tests show that this assumption was violated in all home ranges. Home ranges of pigs in the Valley are unlikely to assume circular conformations because the two plateaus are narrow and the long cliffs on each tend to compress ranges to elongated configurations. The elliptical model of Jenrich and Turner (1969) does not have such a restrictive assumption and calculates an ellipse whose area is expected to include 95% of all points assuming a bivariate normal distribution. This model is robust, reduces the sensitivity of error in the peripheral points in the minimum-area but the elliptical area was found to enclose topographic features and ground not covered by the pig. The modified minimum-area (Harvey & Barbour 1965) has statistical stability inferior to the other three estimators (Jenrich & Turner 1969).

The minimum-area method (Mohr 1947) was chosen from among the four methods used in this study. The minimum area estimates are intermediate between the modified minimum-area and the elliptical area. The minimum area covers all radiolocations for individual pigs, is biased by sample size and is sensitive to movements on the periphery of the home range. Theoretically, this minimum-area should approach the actual home range more closely with increased frequency of locations and with time. The minimum-area has good statistical stability, is graphically the simplest, is the most widely used home range size estimator and has been used by other workers for estimating home range areas in feral pigs (Barrett 1971, 1978; Kurz & Marchinton 1972; Wood & Brenneman 1980).

Topographic features influenced shapes of home ranges. For instance, the western straight line boundary of pig 244 is probably artificial. Straight line boundaries in animals whose home ranges were bordered by the central escarpment were real, as verified from ground checks. However, the actual home range configurations are most likely to be amoeboid. Studies in South Carolina showed similar elongated polygonal home range configurations in the feral populations (Kurz & Marchinton 1972; Wood & Brenneman 1980), but circular home ranges have been reported for the wild boar in Tennessee (Singer et al. 1981). Topographic features influenced shapes of home ranges. With the exception of 850, all upper-plateau home ranges were bordered or nearly so by the Koukouai Gulch and the central escarpment. Both these topographic features have the effect of restricting lateral movement to upslope-downslope movements, so that home ranges tend to be elongated.

Home range size of feral pigs in this study is comparable to that reported by Giffin (1978) for feral pigs in tropical rain forests on the island of Hawaii, but smaller than published home range areas for wild and feral populations in other habitats (Table 32). Thus, size range for feral pig home ranges varies from 1.57-50km, the lower size area results from this study and the upper size area from the studies of Barrett (1971, 1978) and Giles (1978).

Sanderson (1960), in his review on mammal movements, emphasized that home range studies should investigate the reasons for movements. Why then is the home range size of feral pigs in Kipahulu Valley smaller than those in other areas? Several population variables can influence

TABLE 32: Published home range size of feral and wild populations of Sus scrofa.

Location	Habitat	Home range size (km^2)		Reference
		Boars (N)	Sows (N)	
Feral populations				
Hawaii	Tropical koa-ohia rainforest	2.01	1.08	This study
	Tropical rainforest	1.29 - 5.18		Giffin (1978)
	Mountain pasture	5.18 - 10.36		Giffin (1978)
California	Oak-savannah grassland	50	10 - 25	Barrett (1978)
South Carolina	Pine-hardwood plantations, swamps	3.93	1.23 - 7.99	Kurz and Marchinton (1972)
	Pine forest, marshes	2.24	1.79	Wood and Brenneman (1980)
Wild populations				
Tennessee	Hardwood, oak-pine forests, pastoral fields	3.89	3.47	Singer et al. (1981)
	Oak forest, private farms	15 - 19		Lewis (1966)
Australia	Agricultural		18	Pavlov (1980)
	Dry flood plain	10 - 50	5 - 20	Giles (1978)
France	Oak, beech, conifer forest	7	1.19 - 4.24	Mauget (1979a, b)
	Oak, beech, conifer forest		2.9	Spitz and Janeau (1979-per.comm.)

movements. Some breeds of pigs are more sedentary than others (Hafez & Signoret 1969). Density of pigs is known to affect home range size (Jewell 1966). In the present study, sizes of home ranges for pigs in the high density koa forest are smaller than for pigs from the low density ohia forest, thus indicating an inverse relationship between pig density and home range size. Hunting pressure can produce forced movements and increase home range area, but this is considered unimportant. High biological productivity and the availability of living requirements in the non-seasonal rainforest are the most plausible reasons for the localized movements and smaller home ranges of pigs in Kipahulu Valley. Several studies have shown a relationship between spatial distribution of resources and home range size. In arid environments, such as the Sierra foothills in California and the dry flood plains in Girilambone, Australia, movements of feral pigs involved long travels from food to water (Barrett 1971, 1978; Giles 1978). Movements to a source of water is important because pigs do not have functional sweat glands and the need to thermoregulate themselves by wallowing thus becomes "the driving force" (Elton 1966) for movement. Spatial distribution of foods also affects the size of home range (Jewell 1966). When food is abundant in an area, feral pigs prefer to homesite in the vicinity of the food source and thus have smaller home ranges (Barrett 1978; Pavlov 1980). In the montane rain forest in Kipahulu, water is never scarce at anytime of the year. Soils and herbaceous plants are wet continuously from rain or fog drip. Biological productivity is undoubtedly high in this high rainfall, spatially complex tropical habitat. Living requirements (food, water and shelter) are available to the pigs at any point within a 0.5km radius in the koa forest. This reduces the need to move over a larger area, since energy needs can be met within a small area.

Most studies on feral pig movements show that boars have larger home ranges than sows (Pine & Gerdes 1973; Barrett 1971, 1978; Giles 1978). Barrett (1978) attributed home range size dimorphism to the boars' search for breeding opportunities. Other studies in the Southeast showed no difference in size of home ranges between sexes (Kurz & Marchinton 1972; Wood & Brenneman 1980). In this study, boars had larger home ranges than sows, but the home ranges of both sexes in high elevation ohia forest were larger than in pigs from the lower elevation koa forest. Spatial distribution of resources, particularly shelter and food, apparently accounted for home range size differences. On a per unit area basis there are fewer adequate bedding sites (tree holes, caves or overhanging cliffs) in ohia than in the koa forest. Also, in the ohia forest preferred foods of pigs are less concentrated in any one area than in the koa forest.

Hayne's (1949) center of activity (geometric center) that was used to describe feral pigs' home ranges, is a mathematical estimation of the center of the distribution of animal locations. This statistic may not have a biological meaning (Van Winkle 1975). The centers of activity in the upper plateau home ranges were located in between the two research trails rather than on the trails. Field work and tracking studies indicated a centralizing tendency in pig movements toward the interior of the plateau. Although pigs frequently forage along the central escarpment, their centers of activity were unlikely to be sited on it, principally because the escarpment is directly exposed to trade winds during the greater part of a year. The interior of the Valley is more sheltered and this explains why the center of activity is interior to the plateau. Besides, the pig could cover more foraging ground in a shorter distance with a home site in the interior than on the edge of the plateau.

Activity patterns that were interpreted with signal modulations were probably biased towards activity periods. Distinction between foraging and locomotory activities was not consistently possible even though transmitters were custom made with this specification. Daily activity pattern appears to be complex and variable. Pigs had been seen foraging at different hours of the day. Diel activity cycles during the winter months, however, indicated a crepuscular activity pattern. Several observations of pigs resting in early afternoon hours support the conclusion that the pigs forage morning and evening and rest in the afternoon and night. Rain storms reduce activity by confining pigs to the vicinity of a shelter site as indicated by clustering of locations, but activities are generally increased after the rains.

Crepuscular activity patterns have been observed in feral pigs on the island of Hawaii (Baker 1975; Giffin 1978), California (Barrett 1971, 1978) and Australia (Giles 1978). Barrett (1978), citing the works of Hafez and Signoret (1969), pointed out that crepuscular activity is the preferred activity pattern in pigs. In several studies, however, activity patterns were found to change with the season, being preponderantly diurnal during winter, nocturnal in summer and crepuscular in autumn (Kurz & Marchinton 1972; Barrett 1971, 1978). Although diel monitorings were not conducted during summer months, field observations indicate a general year-round adherence to crepuscular activity patterns. Maintenance of this preferred activity and adherence to small home ranges can be attributed to the lack of human (hunting) harassment. Hunting pressure was nil above 730m and infrequent at the upper plateau below 730m.

Lateral movements between Kuikuila, Koukouai Gulch and the lower section of the upper plateau were a surprise and raised initial concern that tagged pigs in the lower koa forest may not be residents on the plateau. Topography in the Gulch area is very rugged, but the pigs can move up steep slopes by taking a path at an angle to the fall line to get to the top of the slope. The movements of two pigs off the plateau into the Gulch were probably dispersal movements, but entry movements into the plateau were either dispersal or forced from hunting pressure in the Cable ridge and in the Gulch area. These movement routes suggest that areas outside the plateau are a source for pigs to enter the lower section of the Valley.

Interplateau movements in the Valley at routes identified above and below Palikea occur infrequently and are used by lower plateau pigs for uphill movements during the strawberry guava season. During the early winter of 1979, upland hunting pressure in the lower plateau below 800m was unusually heavy, and increased trail activity on and below Palikea was observed to result from lower plateau movements to Palikea.

Several management (Chapter 12) and ecological implications can be drawn from this study. Small, compact, sedentary home ranges with stable seasonal centers of activity and extensive home range overlap, show that a small area of the rain forest habitat has sufficient biological productivity and physical components to meet the maintenance needs of feral pigs. Small home ranges and restricted movements will increase in-breeding tendencies, more so if the life-time range of the feral pig does not differ substantially from its annual home ranges monitored in this study. Other than the head and mouth of the Valley, where entry and exit movements are possible, the Valley is a topographic enclave. This feature, together with restricted home ranges, promotes inbreeding and thus, possibly explains population anomalies and lends weight to the hypothesis that body size will decrease with progressive feral existence (Chapter 5). Small home ranges also mean that feral pigs will be more familiar with their home ground than would pigs home-ranging over a larger area. Additionally, the frequency of soil disturbance in a unit area or within a small home range will be greater than in a large home range. Since the hippocampus in the feral pigs increases proportionally with spatial requirements (Chapter 2), it can be hypothesized, from Table 8, that feral pigs in Kipahulu Valley have smaller hippocampuses than feral populations studied elsewhere. When the minimum distance between Palikea and the present upper limit of strawberry guava distribution is measured in home range axis length obtained in this study, a 2.1 range length axis factor shows that pig dispersal of strawberry guava by endozoochory (Chapter 7) must have proceeded via a stepladder progression, wherein the crop established in the home ranges of lower elevation pigs subsequently serve as a seed source for upslope dispersal into higher elevations. Upslope or downslope movements between Palikea and mid-elevation were not borne out in the tracking studies and this, together with observations on scats containing strawberry guava seeds (Chapter 6), support the 2-step ladder pig-aided strawberry guava dispersal hypothesized here.

CHAPTER 10

HEMATOLOGY AND BLOOD BIOCHEMISTRY

Introduction

Hematological and blood biochemical studies have been performed in most North American wild ungulates (Barrett & Chalmers 1977). These studies have aided in understanding population processes, physiological conditions and ecological relationships in natural populations (Franzmann 1972; Seal et al. 1975). Since blood values may vary with race nutrition, age, sex, stress and disease (Dimopoullos 1963), investigators have been able to examine various relationships between an animal's physiological condition and habitat factors (Franzman 1972).

Numerous studies on blood values have been reported for domestic pigs (Dunne & Leman 1975), but very few exist for wild and feral animals. The importance of blood analyses in suid population studies has been shown by four previous works. Williamson and Pelton (1975, 1976) observed that hematological and serological parameters in the free-roaming wild boar could be used as baseline information to compare blood values of the ancestor with its domesticant. Kostelecka-Myrcha (1974) used cellular hematological data to explain the elimination of roan mutants from normal boar populations. McIntosh and Pointon (1981) observed that blood values in an insular population of feral pigs reflected habitat characteristics and adaptation by the animals. Singer and Ackerman (1981) observed that some blood values were correlates of boar conditions during seasons of good or poor acorn production.

None of these previous studies was designed to monitor the health of pigs in their natural environments. Knowledge of the health of animals would have been useful in the management of animal populations since the state of health of the animals invariably affects the decision-making process by dictating the methods, relative urgency and direction of a management program.

The objectives of this study were: 1) to obtain complete baseline hematological and biochemical profiles of the Kipahulu Valley for future comparative studies, 2) to determine the influence of disease or organ dysfunction in the overall health of the population, and 3) to determine any physiological adjustments shown by the pigs to the rain forest habitat.

Materials and Methods

From July 1979 to December 1980, 31 animals (17 females and 14 males) were trapped and each bled once for a blood sample. Three of the females were in the last trimester, three in the second trimester of pregnancy, six were lactating and the reproductive status of the other females was unknown. Eighty-four percent (26) of the study animals were captured on the upper plateau; the altitudinal range for all animals extended from 610 to 1370m.

All blood-sampled animals were derived from the trap line. Traps were usually baited with corn and hapuu (starchy core of tree ferns, Cibotium sp.) which are rich sources of carbohydrates. Captured animals were manually restrained in the lateral recumbent position, their sexes recorded and their ages estimated using tooth eruption and replacement sequence (Matschke 1967). Ages of bled animals ranged from 5 to 36 months. Animals younger than 10 months were considered to be subadults; those older than 10 months were considered to be adults (Williamson & Pelton 1975). Most blood values in pigs are believed to have stabilized by the age of 10 months.

Animals were bled by venipuncture of the anterior vena cava (Carle & Dewhirst 1942; Pond & Houpt 1978), using a 7cm, 18 guage multidraw hypodermic needle fitted to a Vacuumtainer-Leur adapter and evacuated tubes (Becton, Dickenson & Co., New Jersey). Blood was collected into one 3ml Vacuumtainer tube containing ethylenediaminetetracetic acid (EDTA) as the anti-coagulant and into four 10ml Vacuumtainer tubes containing no anti-coagulant. Two peripheral blood smear slides for differential white cell counts and the study of cellular morphology were prepared following the instructions in the 3M 1978 Specimen Preparation Guide. Blood collection tubes were temporarily stored in a thermos bottle until clotting was complete.

The elapsed time between bleeding and serum separation from the blood clot varied from 4-8 hours, depending on the order the animals were bled. Blood samples for biochemical determinations were centrifuged. Three ml whole blood, three ml serum in serum shipping vials containing 3M stabilizers for glucose and enzymes, and two peripheral blood smear slides were then airmailed to Automated Analytical Laboratory Services, Ventura, California. Laboratory methods of blood analyses are shown in Table 33. This service has

TABLE 33: Laboratory methods of blood analyses.

Blood Constituent	Method	Reaction	Instrument
Calcium	Colorimetric	Cresolphthalein-Complexone	SMAC
Phosphorus	Colorimetric	Phospho-Molybdate	SMAC
Glucose	Enzymatic - End Pt.	Hexokinase	SMAC
Urea Nitrogen	Colorimetric	Carbamido-diacetyl	SMAC
Uric Acid	Colorimetric	Phosphotungstate	SMAC
Cholesterol	Enzymatic -	Cholesterol Esterase	SMAC
Total Protein	Colorimetric	Biruet	SMAC
Albumin	Colorimetric	Bromcresol Green	SMAC
Total Bilirubin	Colorimetric	Diazo	SMAC
Alkaline Phosphotase	Colorimetric	P-nitrophenyl phosphate	SMAC
LDH	Enzymatic-kinetic	NAD	SMAC
SGOT(AST)	Enzymatic-kinetic	Aspartate-Alpha keto glutarate	SMAC
SGPT (ALT)	Enzymatic-kinetic	Alanine-Alpha keto glutarate	SMAC
Creatinine	Colorimetric	Picric Acid	SMAC
Iron	Colorimetric	Ferozine	SMAC
Triglyceride	Colorimetric	NADH_NAD	SMAC
Sodium, Potassium	Ion Specific Electrode		SMAC
Chloride	Colorimetric	Mecuric-Thiocynate	SMAC
GGT	Kinetic-Photometric	P-Nitroaniline	SMAC
T_4	RIA	I_{125}	
Differential	Manual		
WBC, RBC	Electronic Counting		Coulter Counter
Hemoglobin	Photometric	Cyanmethemoglobin	Coulter Counter

satisfactorily analyzed similar specimens from other free-ranging ungulates (Matula & Lindzey 1976). Serum samples were also shipped to the State Department of Agriculture, Honolulu, to assay for Leptospira and Brucella antibody titers.

Statistical analysis of the data included calculating the means, standard deviations and 95% confidence levels for each variable. The t-test compared age and sex related differences, and also compared selected mean values in the study population with those in other populations. Statistical analyses assumed that blood values were normally distributed. The Schalm et al. (1975) method of determining the absolute number of each leukocyte cell type from its relative distribution in the peripheral blood smear, given the total leukocyte count, was used to evaluate abnormal leukocyte distribution.

Results

(a) Blood chemistries

Baseline data for 30 biochemical parameters are statistically described in Tables 34 and 35. Several parameters showed a wide range. These were most pronounced for glucose, cholesterol, blood urea nitrogen (BUN):creatinine ratio, iron, triglycerides and total lipids. Many serum enzyme levels such as those for AKP, SGOT, SGPT and GGPT, were also highly variable. Among the cations, calcium was the least variable.

TABLE 34: Statistical description of biochemical parameters for 31 feral pigs in Kipahulu Valley, Maui, Hawaii.

Parameter	Mean	Standard Deviation	Range	95% Confidence Interval	
				Lower	Upper
Calcium, mg/dl	10.20	0.93	8.7- 12.8	9.87	10.52
Phosphorus, mg/dl	8.97	3.07	4.4- 16.0	7.84	10.09
Glucose, mg/dl	107.45	43.35	50.0- 189.0	91.55	123.35
BUN, mg/dl	14.07	11.62	2.0- 46.0	9.83	18.31
Uric acid, mg/dl	0.37	0.17	0.1- 0.8	0.31	0.43
Cholesterol, mg/dl	64.10	17.83	29.0- 100.0	57.57	70.63
Total protein, g/dl	8.13	1.38	6.7- 13.8	7.64	8.62
Albumin, g/dl	3.29	0.30	2.7- 3.9	3.18	3.39
Globulin, g/dl	4.84	1.32	2.8- 10.6	4.37	5.30
Albumin:globulin ratio	0.67	0.16	0.3- 1.0	0.63	0.71
Total bilirubin, mg/dl	0.13	0.07	0.1- 0.3	0.11	0.15
Alkaline phosphatase, U/l	122.52	60.46	50.0- 328.0	100.33	144.31
Lactate dehydrogenase, U/l	685.41	183.33	360.0-1055.0	618.09	752.70
SGOT, U/l	65.72	33.80	15.0- 135.0	53.33	78.10
SGPT, U/l	55.28	29.01	13.0- 145.0	44.65	65.91
Creatinine, mg/dl	1.47	0.42	0.8- 2.2	1.33	1.61
BUN:creatinine ratio	9.78	8.99	1.0- 44.0	4.49	15.07
Iron, µg/dl	190.07	112.45	69.0- 477.0	148.79	231.35
Triglycerides, mg/dl	36.62	15.59	14.0- 70.0	30.91	42.33
Total lipids, mg/dl	261.14	43.19	179.0- 357.0	245.30	276.98
Sodium, mEq/dl	144.34	5.52	136.0- 160.0	142.32	146.36
Potassium, mEq/dl	5.50	1.09	3.9- 8.1	5.12	5.88
Chloride, mEq/dl	100.69	2.87	95.0- 107.0	99.65	101.73
GGTP, U/l	43.59	14.33	29.0- 96.0	38.35	48.83

TABLE 35: Statistical description of hematological parameters for feral pigs in Kipahulu Valley, Maui, Hawaii.

Parameter	N	Mean	Range	Standard Deviation	95% Confidence Interval	
					Lower	Upper
Erythrocytic series						
Erythrocytes, $10^6/mm^3$	25	7.06	5.42- 8.48	0.94	6.68	7.43
Hemaglobin, g/dl	25	14.73	10.14-16.90	1.47	14.13	15.32
Hematocrit, %	25	50.49	35.60-62.10	5.79	48.17	52.86
MCV, μ^3	25	72.04	64.00-89.00	6.96	69.17	74.90
MCH, $\mu\mu g$	25	20.93	18.80-25.50	1.68	20.24	21.61
MCHC, %	25	29.03	25.20-32.90	1.53	28.73	29.64
Leukocytic series						
Leukocytes, $10^3/mm^3$	26	26.77	13.40-39.20	7.14	23.88	29.65
Neutrophils, %	26	56.21	12.00-90.00	20.13	48.03	64.38
Segmentals, %	26	53.50	12.00-80.00	17.88	46.27	60.73
Bands, %	26	2.71	0.00-12.00	4.33	0.95	4.46
Lymphocytes, %	26	31.50	9.00-69.00	16.35	24.88	38.11
Monocytes, %	26	3.08	0.00- 8.00	1.89	2.31	3.84
Eosinophils, %	26	8.33	0.00-22.00	6.86	5.57	11.09
Basophils, %	26	0.92	0.00- 3.00	1.11	0.48	1.35

Thyroid hormones T_3 and T_4 as measured by radioimmunoassay (RIA), averaged 34.35% and 3.36ud/dl (Tables 36, 37). T_3 uptake was more variable than T_4-RIA; the mean T_7 index was 1.05.

(b) Cellular hematology

Hematologic parameters showed high variability as indicated by the wide ranges and relatively large standard deviations. In the erythrocytic series, hematocrit and mean corpuscular volume (MCV) were most variable. It should be noted that an index of anemia, the mean corpuscular hemoglobin concentration (MCHC), was only 29.03 whereas a value of 30 or greater in all mammals is considered normal. Erythrocyte counts, which averaged $7.6 \times 10^6/\text{mm}^3$ were, however, least variable. In the leukocytic series, total leukocyte counts averaged $26.77 \times 10^3/\text{mm}^3$; the highest count was $39.20 \times 10^3/\text{mm}^3$ and the peripheral blood smear differential data indicated that these feral pigs had neutrophilia. Neutrophils dominated over other cell types in the leukocytic series; the mean neutrophil:lymphocyte ratio was 1.78:1. Lymphocytosis (>13,000 cells/dl) was, however, observed in 9.6% (3) of blood-sampled animals. The most extreme lymphocyte:neutrophil ratio was 5.75:1. The neutrophils were principally mature segmented cells which averaged 56.20%; the highest value was 80%. Band neutrophils averaged 2.71% of total leukocyte counts; the highest value was 12%. Basophils were least represented, and averaged only 0.92%. Eosinophil counts ranged from 0-22%, with a mean of 8.33%. Eosinophilia (>72,000 cells/dl) was

TABLE 36: Serum T_3, T_4 values by radioimmunoassay and free thyroxine, T_7 index for 27 feral pigs in Kipahulu Valley, Maui, Hawaii.

Variable	Mean	Standard Deviation	Range	95% Confidence Interval	
				Lower	Upper
T_4-RIA, μg/dl	3.36	1.37	1.1- 7.5	2.85	3.86
T_3 UPTK, %	34.35	4.83	27.7-44.7	32.43	36.26
T_7 Index	1.05	0.40	0.4- 2.1	0.89	1.20

TABLE 37: Normal Serum T_3, T_4 and T_7 values in domestic pigs.

Variable	N	Mean/Range	Reference
T_4-RIA, μg/dl	10	3.32 ± 0.80 (1.70 - 4.68)	Reap *et al* (1978)
	5	4.70 ± 0.45*	Kallfelz and Erali (1973)‡
	2	2.10 ± 0.42†	Kallfelz and Erali (1973)‡
T_3 UPTK, %	5	37.10 ± 1.18*	Kallflez and Erali (1973)‡
	2	32.60 ± 2.20†	Kallfelz and Erali (1973)‡
T_7 Index	5	1.74 ± 0.18*	Kallfelz and Erali (1973)‡
	2	0.69 ± 0.18†	Kallfelz and Erali (1973)‡

* young adult, N = 5

† mature adult, N = 2

‡ T_3 by resin sponge uptake of labelled 3,5,3' - Triiodothyronine; T_4 by competitive protein binding.

observed in 33.30% of the animals. A high eosinophil count was occasionally associated with a lower serum iron concentration.

(c) Age and sex variation

No hematological or biochemical parameters showed any significant sex or age-specific variation. Several biochemical parameters show significant difference between sexes (Table 38) than they did between subadult and adult age classes (Table 39).

(d) Abnormal erythrocyte morphology

Abnormal morphological variations in erythrocyte shape, size and color were identified from peripheral cells in blood smears. Poikilocytosis, the deviation of erythrocytes from their normal shape, was seen in two animals and took the form of burrs. Hypochromasia and polychromasia were also observed, with the latter condition occuring more frequently. Anisocytosis occurred in 45% (14) of the animals where the aberrant cell types were microcytes. Marked microcytosis was observed in two animals. Serum iron concentration in these markedly microcytic animals was at the lowest level recorded (77.00mcg/dl) as opposed to the sample mean of 190.07mcg/dl. Markedly microcytic animals were also hypochromic. Nucleated red blood cells (NRBC) present at lNRBC/100WBC and 2NRBC/100WBC were observed in the peripheral blood smears of two animals. Except for polychromasia, none of these abnormalities have been reported from free-ranging pigs studied elsewhere.

TABLE 38: Serological parameters of feral pigs that show differences between sexes.

Parameters	Mean ± S.D.		t
	Males (N=14)	Females (N=17)	
Uric acid, mg/dl	0.32 ± 0.14	0.40 ± 0.18	26.67, $P < 0.001$
Total proteins, g/dl	8.47 ± 1.76	7.85 ± 0.85	2.67, $P < 0.05$
Albumin, g/dl	3.30 ± 0.34	3.26 ± 0.26	3.48, $P < 0.01$
Globulin, g/dl	5.17 ± 1.72	4.58 ± 0.78	2.73, $P < 0.05$
Albumin : Globulin ratio	0.64 ± 0.15	0.69 ± 0.14	18.52, $P < 0.001$
Total bilirubin, mg/dl	0.14 ± 0.08	0.12 ± 0.05	40.00, $P < 0.001$
Creatinine, mg/dl	1.53 ± 0.33	1.42 ± 0.47	4.96, $P < 0.001$
Potassium, mEq/dl	5.75 ± 1.27	5.30 ± 0.86	3.06, $P < 0.01$
T_4-RIA, mcg/dl	3.04 ± 0.91	3.61 ± 1.60	2.45, $P < 0.05$

TABLE 39: Serological parameters of feral pigs that show significant differences between age classes.

Parameters	Mean ± S.D.		t
	Subadults*(N=13)	Adults (N=18)	
Total proteins, g/dl	7.26 ± 0.59	8.83 ± 1.42	3.75, $P < 0.001$
Globulin, g/dl	5.47 ± 1.40	4.06 ± 0.61	3.39, $P < 0.01$
Albumin : Globulin ratio	0.76 ± 0.14	0.58 ± 0.10	4.18, $P < 0.001$
Triglycerides, mg/dl	42.25 ± 15.74	19.69 ± 12.23	2.39, $P < 0.05$
Total lipids, mg/dl	281.37 ± 38.29	236.23 ± 35.08	3.35, $P < 0.01$

* Subadult and adult age class divisions are after Williamson and Pelton (1976).

Discussion

Stress and its effects on blood biochemical hematologic parameters are problems inherent in all studies using free ranging animals. Animals generally exhibit a normal physiological stress response when captured, handled and bled. Hence, the interpretation of blood chemistries and hematology can be spurious if these variations are not distinguished from those produced by pathological factors. Results in this study are interpreted by discussing major sources of variations and the relative importance of each in this study.

(a) Sources of variation

Variations in blood parameters are generally produced by the following factors: 1) stress associated with capture, immobilization or handling (Franzmann & Thorne 1970; Williamson & Pelton 1975, 1976; Matula & Lindzey 1976; Barrett & Chalmers 1977); 2) age, sex and reproductive condition (Coles 1980); 3) blood collection techniques, storage and analytical methods (Wintrobe 1967; Kaneko 1980); 4) nutritional status of animals (Doxey 1971; Singer & Ackerman 1981); 5) breed-types (Payne et al. 1974; Pond & Houpt 1978); 6) environment (Coles 1980); and 7) disease (Dunne & Leman 1975). Two other sources of variation identified in this study were hemolysis and bacterial contamination in several serum samples.

Stress factors probably accounted for some of the variability in serum biochemical (Tables 34, 36) and hematological (Table 35) values. During restraint, feral pigs were very active, visibly excited and made repeated attempts to escape by charging their snouts into the sides of the trap to the point of self injury. In fact, bleeding of the nasal plate was sometimes observed. Increased excitability and forced activity are known to elevate serum enzymes, glucose and cholesterol in wild ungulates (Barrett & Chalmers 1977). Handling stress, therefore, may probably have elevated SGOT, SGPT, GGTP, LDH, AKP cholesterol and glucose levels. LDH measured in this study as high as 1055U/l; transaminases increased to 145U/l (Table 34). Glucose averaged 107.45 plus or minus 43.35mg/dl; the highest concentration was 189mg/dl.

Nutritional status and dietary composition of the animal's last meal could also affect several blood biochemical values. When acorns were abundant, the serum levels of total proteins, albumin, cholesterol and the A:G ratio in the wild boar in Great Smoky Mountains National Park (GSMNP) was significantly higher than during acorn failure (Singer & Ackerman 1981). The levels for glucose and total lipids would be affected by diets, too. Animals in this study, trapped with baits rich in carbohydrates, were bled the morning after this meal and, hence, gave normal or high glucose levels in general. Depressed glucose level (50mg/dl) in some animals was probably due to factors other than the nutritional status of the animals. Bacterial growth was reported in some serum samples with low glucose levels. Although the presence of erythrocytes could also drastically lower glucose levels, depressed levels were most likely produced principally by the bacterial growth rather than by the length of time serum and clots remained in the samples (Green 1980 Ventura, California - pers. comm.).

Pain during venipuncture could alter certain blood parameters (Pond & Houpt 1978). Other workers have bled pigs from the tarsal veins (McIntosh & Pointon 1981), jugular, cephalic, auricular, orbital, and coccygeal veins or even by tail amputation (Pond & Houpt 1978). Sampling blood from the anterior vena cava did not appear to produce discomfort to the animal as much as restraint itself did. Heart puncture was initially used in this study to collect blood from the first five animals, but none of these blood samples could be used because of severe hemolysis. Blood drawn from the anterior vena cava is less prone to hemolysis (Carle & Dewhirst 1942) than from the ear vein or other bleeding sites (Hoerlein et al. 1951). However, slight hemolysis occurred, nevertheless, in four samples. In addition, serum was routinely separated from the blood clot only after 4-8 hours. Additionally, the erythrocytes of pigs are very fragile and prone to hemolysis (Hoerlein et al. 1951). Agitation from backpacking, transportation and heat probably brought about the hemolysis. Serum potassium, inorganic phosphorus and LDH were slightly elevated in these hemolysed samples.

Age and sex related differences in serum biochemical and hematological parameters have been evaluated in domestic pigs. Total proteins, globulin, A:G ratio, calcium, AKP and inorganic phosphorus concentrations were greater in the serum of male than female pigs (Tumbleson et al. 1969). In this study, no hematological value showed age or sex differences. This result is consistent with boar studies in Tennessee (Williamson & Pelton 1976) and GSMNP (Singer & Ackerman 1981).

Total proteins and the A:G ratio were higher in adults than in subadults. The boars in Tennessee showed age related differences for total proteins, albumin, sodium and chloride concentrations (Williamson & Pelton 1975). Age differences may be due to differences in the nutritional state or in the activity of the hematopoietic systems between subadult and adult pigs. In contrast to the boar in Tennessee, feral pigs in this study showed several sex related differences in serum biochemical values. These differences may be due to reproductive status condition of the sows, lactation stress and diet.

(b) Comparison between domestic, feral and wild populations

Serum biochemical values compared favorably with those in other populations (Table 40). Differences in some biochemical values were probably due to dietary differences and stress factors. Phosphorus levels fell within the normal range of values in domestic pigs but were higher than in Kangaroo Island (K.I.) strain feral pigs. LDH and transaminases were much higher than the normal range for domestic pigs and K.I. feral pigs. These elevated values were probably produced by the stress factors already discussed. Cation concentrations fell within the normal range of domestic pigs, and compared well with those in other populations. Cholesterol was much lower than in K.I. feral pigs; this was probably due to the grower ration on which K.I. feral pigs were maintained. The A:G ratio was higher than in domestic pigs but lower than in all other normal populations. Variations in albumin and globulin concentrations are normally produced by dietary protein deficiency, nutritional imbalances and vitamin deficiencies (Pond &

TABLE 40: Comparison of selected biochemical parameters (means and/or range) for feral, wild and domestic pigs.

Population	Feral pigs	European wild boar	European wild boar*	Feral pigs†/‡	Domestic pigs
N	31	33	37	19	
Age (months)	5-36	1.5-26	1.5-26	3-24	3-36
Calcium (mg/dl)	10.20			11.60	7.1-11.6[1]; 9.0-12.5[9]; (10.2-11.9)[10]
Phosphorus (mg/dl)	8.97			7.12	5.3-9.6[1]; 4.6-10.2[9]
Glucose (mg/dl)	107.45	107.29	90.79	124.30	85.0-150.0[1]; 118.0[13]
BUN (mg/dl)	14.07	10.52	14.06	15.41	10.0-30.0[1]; 8.0-24.0[12]
Cholesterol (mg/dl)	64.10			104.4	36.0-54.0[1]; 57.0-160.0[2]; 64.0-104.0[10]
Total Serum Protein (g/dl)	8.10	7.14	8.99		7.9-8.9[1]; 6.3[12]; 6.9[13]
A:G	0.67	0.90	0.41	1.27	0.37-0.51[1]
Total Bilirubin (mg/dl)	0.13			0.15	0-0.6[1]; 0.4-1.17[2]; 0.2[8]; 0-0.4[9]
AKP (U/l)	122.52			109.00	118.0-395.0[1]; 71.0-110.05[4]+; 97.9 (61.7-14 2)[10]
LDH (U/l)	685.41			456.00	499.0[1]; (380.0-634.0)
SGOT (U/l)	65.72				32.0-84.0[1]; 14.8±6.7[3]; 13.9[4]; 14.0±7.5[5]; 11.0-13.0[6]
SGPT (U/l)	55.28				45.0[1]; (31.0-58.0); 25.0±7[7]; 12.9±3.8[3]; 10.0±2.7[5]
Creatinine (mg/dl)	1.47			1.22	1.0-2.7[1]; 1.0-2.7[9]
Iron (µg/dl)	190.07				91.0-199.0[1]; 121.0±33.0[11]
Total Lipids (mg/dl)	261.14				272.0-447.0[2]
Sodium (mEq/l)	144.34	142.00	141.33	146.0±3.3	135.0-150.0[1]; 110.0-154.0[10]; 146.0[13]
Potassium (mEq/l)	5.50	6.78	8.67	5.4±0.9	4.4-6.7[1]; 3.5-5.5[10]; 4.7[13]
Chloride (mEq/l)	100.69	97.10	100.18	101.9±3.1	94.0-106.0[1]; 88.0-115.0[10]; 104.0[13]
Reference	THIS STUDY	Williamson & Pelton 1975, 1976	Williamson & Pelton 1975, 1976	McIntosh & Pointon 1981	See below

* Pen-reared.

\+ Converted to International Units from King-Armstrong Unit by multiplying conventional unit by a factor of 7.10.

† Feral history of 180 years on Kangaroo Island, Australia, but blood-sampled animals are derived from a piggery.

‡ SI Unit converted into conventional unit using conversion factors in Kaneko (1980), p.787.

[1] Kaneko (1980)
[2] Pond and Houpt (1978)
[3] Cornelius <u>et al</u> (1959)
[4] Cysewski <u>et al</u> (1968)
[5] Ostadius <u>et al</u> (1959)
[6] Witzel <u>et al</u> (1967)
[7] Zimmerman <u>et al</u> (1965)
[8] Doxey (1960)
[9] Kelly (1974)
[10] Baetz and Mengeling (1971)
[11] Melby and Altman (1974)
[12] Medway (1969)
[13] Tumbleson (1969)

Houpt 1978). Infection could have elevated globulin and depressed albumin levels, thus altering the A:G ratio (Payne 1976). In pigs, chronic anteric disease, including chronic iteitis (Nielson 1966), may produce excessive plasma albumin loss and hence yield an A:G ratio with a value of less than one. It was unlikely that A:G variations were due to protein deficiency (see below).

(c) Physiologic health: Total leukocyte count and differential cell data

Leukocyte count in healthy domestic pigs is very variable (Pond & Houpt 1978). The total leukocyte count in the study animals was considerably higher than the normal range of values for domestic pigs (Table 41). Mean leukocyte count was significantly higher than in the free-roaming [$P(t > 9.68) < 0.001$; df=62] and pen-reared boar [$P(t > 3.68) < 0.001$; df=66] in Tennessee, the boar in GSMNP during the abundance of acorn [$P(t > 8.11) < 0.001$; df=72] and in K.I. strain feral pigs [$P(t > 9.07) < 0.001$; df=48] in Australia. Additionally, this study population was leukocytic (>22,000 cells/μl). Leukocytosis does not characterize the K.I. feral animals or GSMNP, Polish and Tennessee wild populations.

Sometimes the health of animals may be assessed solely from total leukocyte count, but differential cell types are often more revealing. Since any interpretation or conclusion on population health from differential cell data hinges on the accuracy of total leukocyte count, it is necessary to first consider the nonpathologic factors in this

TABLE 41: Comparison of leukocytic variables (mean and/or range) for feral, wild and domestic pigs.

Population	N	Age months	WBC $10^3/mm^3$	Bands %	SEGS %	Neutrophils %	Lymphocytes %	Monocytes %	Eosinophils %	Basophils %	References
Feral pigs (Hawaii)	31	5-36	26.77	2.71	53.50	56.21	31.29	3.22	8.33	2.00	THIS STUDY
European wild boar (Tennessee)	33	1.5-26	12.24			54.78	40.81	2.95	1.52	0.07	A
European wild boar* (Tennessee)	37	1.5-26	18.82			37.38	55.70	3.22	3.62	0.05	A
European wild boar (Poland)	6	2.1	15.35			74.00	25.20	0.80	0		B
European wild boar† (Poland)	11	2.4	14.48			60.40	38.60	0.70	0.30		B
Feral pigs‡ (Australia)	19	3-24	13.80								C
Domestic pigs		5-36	15-20^{1}	0-2^{7}	37.00^{3}	58.00^{1}	36.80^{1}	1.90^{1}	2.30^{1}	0.30^{1}	See below
					(28-47)						
			18.00^{8}	1.0^{9}	40-60^{7}	39.00^{6}	53.00^{3}	5.00^{3}	3.00^{3}	1.20^{6}	
			(10-23)	(0-4)		(30.0-50.0)	(29.0-62.0)	(2.0- 5.0)	(1.0-11.0)	(0.0-4.0)	
			16.00			32.00^{8}	52.00^{6}	3.30^{6}	4.50^{6}	0^{7}	
			(11-22)				(40.0-60.0)	(1.0-10.0)	(1.0-10.0)		
						37.00^{9}	53.00^{9}	2-8^{7}	1-5^{7}	0.50^{8}	
			(10-20)^{6}			(28.0-47.0)	(39.0-62.0)				
			15.50^{10}			39.00^{10}	30-50^{7}	5.00^{9}	3.80	0.50^{9}	
			(10-21)			(30.3-47.7)		(2.0-10.0)		(0.0-2.0)	
							59.00^{8}	5.00^{8}	3.50^{9}		
									(0.5-11.0)		
							52.10^{10}	3.30^{10}	4.50^{10}	1.20^{10}	
							(43.1-62.9)	(2.4- 4.1)	(2.1- 6.9)	(0.6-1.8)	

* Pen-reared

† Roan individuals

‡ Feral history of 180 years on Kangaroo Island, Australia, but blood-sampled animals are derived from a piggery.

Key to Reference:

A Williamson and Pelton (1975, 1976)
B Kostelecka- Myrcha (1974)
C McIntosh and Pointon (1981)

TABLE 41(contd.): Comparison of leukocytic variables (mean and/or range) for feral, wild and domestic pigs.

Key to notations:

Wirth (1950)
Giltner (1907), N = 24, Age = 4 months
Medway (1961)
Miller (1961), Age = 4 months
Pond and Houpt (1978)
Scarborough (1931), for adult pigs
Kelly (1974)
Doxey (1971), for conventional and miniature pigs
Schalm (1965)
Mitruka and Rawsley (1977), for male animals, mini pigs 70-100kg.

study and their importance in affecting leukocyte counts. In the present evaluation, leukocytosis in the study animals was considered to be a clinical reflection of the health of the pigs, rather than due primarily to physiological stress causes. Comparison of leukocyte counts with other populations is considered valid because stress factors in this and other studies were similar. Feral pigs were trapped, handled and bled with methods similar to those of Williamson and Pelton (1975, 1976) in Tennessee. Sample sizes and ages of animals in their boar studies were comparable to those of this study. Effects of handling stress on leukocyte counts may be assumed to be a common denominator to this and the Tennessee studies. However, the GSMNP boar studies included animals bled, after being shot, by heart puncture (Singer & Ackerman 1981). In that study the total leukocyte counts were lower than those for the feral pigs in this present study. Pregnancy may elevate leukocyte counts, but while this physiologic response is an important source of variation in cows and dogs, it is less important in pigs (Coles 1980). Leukocytes also increase in numbers an hour after feeding. Stage of digestion was not considered a significant factor influencing leukocyte counts in this study because pigs ate the food-baits soon after capture, and more than an hour would have elapsed between the last feed and blood sampling.

Pathologic factors that produce leukocytosis are disease, infection and parasitism (Dunne & Leman 1975; Coles 1980), and microbial milieu in the animal's home range. When these factors are reduced or absent, leukocyte counts can be expected to be low. Disease-free feral pigs derived from a stock experimentally treated with streptomycin, penicillin and an antihelminthic drug, had low (13.80 x $10^3/mm^3$) total leukocyte count (McIntosh & Pointon 1981). The microbial milieu in the rain forest habitat could have caused leukocytosis. Restricted home ranges of feral pigs have two consequences: 1) the frequency of animal encounters, and 2) the intensity of home range use per unit area of home range size, are greater in smaller home ranges. These factors presumably facilitate the localization of pathogens and their transmission among animals. Leukocytosis in the study animals may, in part, be a reflection of the population response to these phenomena. Supportive evidence may be drawn from two other studies. Leukocyte counts tend to increase when large groups of pigs are housed together; but pigs kept in minimal disease herds have lower total leukocyte counts than pigs kept under ordinary commercial conditions (McTaggart & Rowntree 1969). Wild boar that were pen-reared had higher total leukocyte counts than free-roaming animals (Table 41). Williamson and Pelton (1976) attributed the higher counts in pen-reared boars to their confinement in a small area, which increases the tendency of pathogens becoming concentrated in one area and disseminating to all confined animals.

Differential cell counts support this tentative conclusion that leukocytosis in the study animals was probably pathological rather than physiological. Leukocytosis was observed to be in consequence to increases in granulocytes (Table 41). This blood profile is in contrast with that in domestic pigs where leukocytes are represented by more agranulocytes (lymphocytes) rather than granulocytes. Neutrophil count 56.21% (12-90) was in excess of 10,000 cells/µl; the study animals were therefore neutrophilic. Neutrophilia is caused by bacterial, fungal or viral infections and intoxications. Fungal infection appears to be unimportant because monocytosis was not evident in the blood profile. Neutrophilia did not characterize the Tennessee populations (contra Williamson & Pelton 1976) or Kangaroo Island feral pigs, but occurred in the Polish boar; the absolute neutrophil cell density in the Polish boar was, however, less than in the feral pigs in this study. The study population was, therefore, in clinically poorer health than animals in other populations. Neutrophils were predominantly segmented cells; these differential data are indicative of a disease factor. Pathologic leukocytosis is generally associated with an increase in segmented neutrophils (Coles 1980). Band neutrophils are very rare in domestic pigs and extremely rare in the wild boar (Williamson & Pelton 1976), but were high in the study animals. Band neutrophils are released into the blood circulation from the bone marrow only when animals respond to some disease factor (Coles 1980).

Although the study animals were neutrophilic, lymphocytosis was observed in only three animals; increase in lymphocytes normally occurs during the recovery stages of certain infections (Coles 1980). Eosinophils exceeded 2000 cells/µl; the study animals were therefore eosinophilic. Absolute eosinophil cell counts were higher than in domestic pigs and the Tennessee populations. Pigs with high eosinophil counts were occasionally associated with low serum iron, and in four autopsied animals, heavy infestations of Stephanurus dentatus were found. Among the three stress factors (nutrition, parasitism and handling) that commonly elevate neutrophilia, parasitic infections invariably produce eosinophilia (Doxey 1971; Coles 1980) as do allergic or anaphylactic reactions. Eosinophilia in the study animals was most likely due to tissue invasive parasites, the important nematodes being Stephanurus dentatus, Metastrongylus elongatus and Ascaris lumbricoides.

Abnormal erythrocytic forms seen in the stained blood smears may have resulted from either increased erythrogenesis or irregularities in erythrocyte maturation. Polychromatic erythrocytes appear to be common in domestic pigs (Wisecup & Crouch 1962) and the wild boar (Williamson & Pelton 1976). Microcytes are indicative of iron deficiency (Doxey 1971). Markedly microcytic erythrocytes which were also hypochromatic are manifestations of microcytic anemias. This, however, does not appear to be the case. Although serum iron concentrations in these animals were very low (77mcg/dl), hemoglobin, MCV, MCH and MCHC concentrations were not depressed below the normal range of values in domestic pigs (Table 42). Dietary iron is probably abundant in the forest soils although it often is in a form not utilized by plants. T_3 thyroxine and T_4-RIA levels were normal (Table 36, 37) suggesting no iron deficiencies in the animals. However, depressed levels of iron may have been produced by the heavy lice infestation and especially by the heavy intestinal parasite loads observed at necropsy. Other factors known to affect iron metabolism and produce microcytic anemias are copper deficiency, molybdenum and bracken fern poisoning (Coles 1980).

TABLE 42: Comparison of erythrocytic variables (mean and/or range) for feral, wild and domestic pigs.

Population	N	Age months	Platelets $10^3/mm^3$	RBC $10^6/mm^3$	HGB g/dl	HCt %	MCV μ	MCH μμg	MCHC %	References
Feral pigs (Hawaii)	31	5-36	360.33	7.06	14.73	50.49	72.04	20.93	29.03	THIS STUDY
European wild boar (Tennessee)	33	1.5-26	323.17	7.26	14.82	39.02	54.48	20.81	27.20	Williamson and Pelton (1975, 1976)
European wild boar* (Tennessee)	37	1.5-26	418.03	7.72	15.22	42.16	55.03	19.92	27.65	Williamson and Pelton (1975, 1976)
European wild boar (Poland)	6	2.1		6.76	16.00	45.90	69.06	24.00	35.04	Kostelecka-Myrcha (1974)
European wild boar† (Poland)	4	2.4		6.33	17.50	48.00	77.06	28.15	36.77	Kostelecka-Myrcha (1974)
Feral pigs‡ (Australia)	19	3-24		8.80	16.30	47.00	53.60		34.60	McIntosh and Pointon (1981)
Domestic pigs		5-36	200-500[2]	5.0-8.0[1]	13.00[2]	42.00[2]	60.05[4]	19.90[4]	27-40[5]	See below
						(32.0-50.0)				
			400.00[8]	6.80[7]	14.00[8]	42.00[8]	63.00[9]	20.00[9]	32.00[9]	
			(250-700)	(5.0-8.5)	(11.0-17.0)	(37.0-50.0)	(50-68)	(17-23)	(30-34)	
			300.00[10]	7.20[8]	13.00	43.20	60.00[10]	18.30[10]	30.10[10]	
			(232-368)	(6.0-9.0)	(10.0-16.0)	(42.4-44.2)	(58-62)	(18-19)	(26-34)	
				7.09[10]	10.11[7]	39.60[7]				
				(5.5-8.7)	(8.3-12.7)	(32.2-46.3)				
					13.00[10]					
					(12.5-13.5)					

* Pen-reared

† Roan individuals

‡ Feral history of 180 years on Kangaroo Island, Australia, but blood-sampled animals are derived from a piggery.

Nucleated erythrocyte (NRBC) are usually found only in bone marrow in healthy adult animals and appear in the peripheral blood only in diseased animals in response to anemias in remission, tumors, or toxic compounds from bacteria or ingested food (Schalm et al. 1975).

(d) Protein status

Several blood chemical values have been used as condition indicators and for evaluation of protein status in wild ungulates. BUN increases with increased intake of dietary protein (Coles 1980). It is less influenced by handling stress (Seal et al. 1972). Total proteins are directly influenced by nutritional levels (Dimopoullos 1963), although this chemical value may be relatively insensitive as a condition correlate in some ungulates (Seal et al. 1975). When examined together, albumin, hemoglobin and BUN become a more valid diagnostic test for protein status; depressed levels of all three parameters are usually indicative of a protein deficiency (Payne 1981). Levels of these three proteins in the Kipahulu Valley population compare favorably with the normal range of values (Kaneko 1980:792-797) in domestic pigs. BUN was higher than in the boar in GSMNP (BUN = 11 ± 3mg/dl) (Singer & Ackerman 1981) and the Tennessee populations, but was lower than the K.I. strain feral pigs (Table 40); the higher BUN in K.I. pigs was due to the relatively rich dietary protein in growers ration on which the experimental K.I. pigs were maintained (McIntosh & Pointon 1981). BUN in this study was, however, very variable. Catabolic breakdown of tissues could increase BUN (Medway et al. 1969). Very low BUN was recorded from lactating sows. Lactation may be viewed as a drain on the sow's proteins, and hence the lower BUN. Total serum protein was higher than in the boar in GSMNP during abundant acorn (7.0 ± 0.3g/dl) (Singer & Ackerman 1981) and free-roaming boar in Tennessee; but lower than pen-reared boar fed with corn (Table 40). These comparisons indicate an adequate nitrogen intake and a normal total protein status of the feral pigs in the rain forest habitats.

(e) Kidney, liver and thyroid functions

BUN and creatinine may increase to very high levels following kidney damage (Medway et al. 1969). None of these indices, however, were abnormal in the feral pigs in this study, even though abscesses were noted in some kidneys at necropsy from parasitism by S. dentatus. Liver function is normally assessed from specific serum enzyme levels and other specific biochemical tests. Bilirubin levels will increase in obstructive liver diseases including parasitic obstruction of bile ducts or starvation (Cornelius 1980). Bilirubin levels were normal in the pigs in this study; values obtained compared favorably with normal values in other domestic pigs. Serum enzymes were, however, considerably elevated. Elevation of SGOT in pigs have been reported for bile duct obstruction, aflatoxicosis (Cysewski et al. 1968), hepatic necrosis and diseases of the cardiac and skeletal system (Cornelius et al. 1959). Ostadius et al. (1959) found that SGOT rose to 87 U/l and SGPT to 45 U/l following liver dystrophy. Although serum enzymes were considerably elevated, a conclusive statement on dysfunction of any one organ seems unwise. SGOT does not occur in especially high concentrations in pig liver and is found in other major tissues. Hence, elevated SGOT need not necessarily imply liver disease. Despite their non-tissue specificity, SGOT, SGPT, AKP and LDH have been found to be useful in diagnosing liver dysfunction in dogs and cats, but the use of these enzymes in assessing liver function in pigs has to be done with caution (Cornelius 1980). While these elevated enzyme levels in the study animals may also be indicative of some nematode-induced liver dysfunction, other extrinsic factors already discussed are also equally likely contributors to these elevated values.

T_3 thyroxine and free thyroxine T_4-RIA are two principal thyroid hormone assays for assessing thyroid functions (Reap et al. 1978; Kaneko 1980). Both thyroid hormone levels compare favorably with the normal range of values found in domestic pigs, suggesting an adequate thyrometabolic status in the study animals. Caution should be used in comparing thyroxine values (Tables 36, 37) because thyroid determinations are method specific.

Blood profiles indicated that nitrogen intake and the protein status of the feral pigs were adequate. Neutrophilic leukocytosis characterized the feral pigs in this study population, but not in other boar and feral populations. It is suggested that although condition indicators (BUN, total proteins, albumin, hemaglobin) of feral pigs were relatively good, the clinical health of the study population is poorer than pigs in other free-ranging populations. Leukocytosis was probably in response to some disease factor, tissue invasive parasites or microbial milieu in home ranges.

CHAPTER 11

SOURCES OF MORTALITY

Field evidence of mortality was scant. Examples were isolated and mostly circumstantial in nature. Sick, debilitated or dying pigs were never encountered. Pig skulls or dead animals were seldom located and remains of only six animals were found on open ground, in caves and in tree holes (Table 43). While the ages at death of these specimens could be determined, the sources of mortality were unknown. The predatory role of feral carnivores (dogs and mongooses) was established, however, from direct sight observation. Sources of mortality identified were from physical causes (accident, entrapment, weather), living organisms (parasites, dento-alveolar diseases, predators) and welfare factors (food, water, cover). These are discussed here for their relative importance in influencing animal numbers.

Entrapment in Mud

Three separate groups of five piglets, each about one week old, were found mired helplessly in mud. Mud-entrapped piglets are highly susceptible to hypothermia, starvation or predation by feral carnivores. This source of mortality may be important in removing over 50% of a sow's litter. It is unlikely that a sow would extricate an entrapped offspring or be concerned for a stray piglet so long as she has at least one piglet to nurse.

TABLE 43: Data on feral pigs which died from natural causes.

Location	Pig remains			
	Description*	Site	Age at death (year)	Source of mortality
K628	skull, parts of skeleton	tree hole	0.16	unknown
K634	partly broken mandible	overhanging cave	1.16	unknown
E870	skull and whole skeleton	open ground	0.66	unknown
E927	decaying carcass**	tree hole	0.66	unknown
E1226	skull, few vertebrae	open ground	0.83	unknown
GS1037	skull only	tree hole	0.50	unknown

* Made at first sighting of pig remains.

** Carcass about a week old and without external signs of body mutilation or abnormalities.

Weather

The weather could be a source of mortality: (1) indirectly as a predisposing factor in the loss of sick animals or stray piglets, and (2) directly as a source of mortality of newborn piglets. Pigs generally continue to forage during rainy weather, but typically take shelter in available tree holes and uluhe thickets at foraging sites during the heaviest rains. Because extended periods of rainfall for periods of a week or more are not unusual, especially during winter months, animals may be forced to forage even in stormy weather. Diseased animals, such as those suffering from helminth-produced pneumonia, may be more predisposed than healthy animals to death by exposure to rain or cold. Since weather contributes to mortality in already weakened animals, its overall influence in population mortality is only to hasten death in those animals which are less adapted to long-term survival.

Newborn piglets leave the farrowing nest 1-2 weeks postpartum (Barrett 1971). Farrowing nests in the ohia forest are generally sited in open places, are not weather-proof and are prone to flooding. Thus, sows may be forced to evacuate their litters from their nests earlier than usual. Although feral piglets are more resistant to cold than domestic pigs because of a denser pelage and more mature metabolic response (Foley et al. 1971), nest flooding, direct exposure to rain and chill factors could be a direct mortality factor resulting from early evacuation from the farrowing nest. The mean annual temperature in the ohia forest is 15.0°C (8.1-21.1°C). Death by convective heat loss can be important whenever piglets were separated from the sow. Weather probably contributed to juvenile mortality by acting in combination with nest or cover inadequacy.

Parasites

Free-ranging pigs world-wide are hosts to 26 nematode parasites (Bernard & Biesmans 1978), several cestodes (Ineson 1953; Sweatman & Williams 1962; Barrett 1971; Hatsushika et al. 1977; Giffin 1978) and trematodes (Ineson 1953; Babero et al. 1959; Foreyt et al. 1975). Information on the prevalence of a parasite fauna in natural populations could be useful in assessing the well-being of animals and the importance of parasites as a source of mortality.

Necropsied animals were surveyed for parasite prevalence by dissecting the following structures and making gross examinations for infection sites and parasite lesions: 1) lungs, trachea, diaphragm, bronchi and bronchioles, 2) liver and gall bladder, 3) kidneys, ureter and urinary bladder, 4) small and large intestines, and 5) stomach. Occurrence of the trichina worm (Trichinella spirella) was determined by stretching, with both hands, the cut-out diaphragm and searching it for any white cyst (Alicata 1979 - pers. comm.). Visual estimates of the numbers of a parasite were made to categorize infestations as light (<10 worms per host), moderate (11-50) or heavy (>50) (Babero et al. 1959). In addition to collecting observed parasites and diseased tissues for identification, fecal samples were taken and examined for protozoan parasites using standard salt flotation techniques.

Feral pigs in Kipahulu Valley were parasitized by at least two ectoparasites, three protozoans and seven nematodes (Table 44). Cestodes, trematodes and the trichina parasite were not detected. Each infected animal hosted at least two nematode parasite species and most animals had three or more parasites in all. Six pigs (15.7%) were parasitized by a total of five internal parasites.

The pig louse (Haematopinus suis) was the most common ectoparasite, occurring in 85.4% (41) of animals. Newborn piglets (1-2 weeks old) had lice on their coats--lice infection must have been from their nursing mothers. Two generations of lice were often recognizable on infected adult pigs. The ears, dorsal spines, and the skin between the legs and on the abdomen were the most heavily infested sites. Lice eggs were observed in 37.5% (18) of lice-infected pigs. The spinal bristles in the dorsal mane appeared to be the egg-laying site for the parasite. The mange mite (Sarcoptes scabiei) and an unidentified mite were the other ectoparasites found in three pigs. The skin at mange-infected sites was scaly and only thinly covered by hairs. Adult mange parasites and their eggs were recovered from epidermal scrapings. Mange infections were localized and did not appear to be important.

The lungworm (Metastrongylus elongatus) and the kidney worm (Stephanurus dentatus) were the two most prevalent internal parasites, occurring in 89.4% (34) and 81.5% (31) of the sample population,

TABLE 44: Prevalence and intensity of parasite infestation in feral pigs in Kipahulu Valley.

Parasite	Infection site	Number infected (N)	Intensity of infection**(%)			Percent infected
			Light	Moderate	Heavy	
Protozoa						
Balantidium coli	encysted in feces	1(20)	100.0			5.0***
Coccidia	encysted in feces	12(20)	25.0	58.3	16.6	60.0***
Sarcocystis sp.	encysted in feces	1(20)	100.0			5.0***
Arthropoda						
Haematopinus suis	body, mostly ears, and abdominal skin	41(48)	19.5	36.5	43.9	85.4
Sarcoptes sp.	epidermis of skin	3(48)	100.0			6.2
Nematoda						
Ascaris lumbricoides	small intestine	13(38)	30.7	69.2		34.2
Metastrongylus elongatus	lung alveoli, trachea, bronchi, bronchioles	34(38)	14.7	47.0	38.2	89.4
Oesophagostomum sp.	large intsatine, caecum	25(38)	12.0	56.0	32.0	65.7
Physocephalus sp.	stomach wall	3(38)	100.0			7.8
Stephanurus dentatus	perirenal fat, liver, kidneys, ureters, bladder, lungs, lumbar muscles	31(38)	25.8	35.4	38.7	81.5
Strongyloides sp.	small intestine	6(38)	100.0			15.7
Trichuris suis	large intestine, caecum	12(38)	13.3	66.6		31.5

* 14 to 25 x 12 to 20 μ

** Expressed as a percentage of the total number of parasitized pigs in sample.
Light = < 10 parasite per host
Moderate = < 50 parasite per host
Heavy = > 50 parasite per host
(Babero et al. 1959)

*** Based on 20 fecal floatations.

respectively. Adult lungworms were restricted to the respiratory apparatus where they were commonly seen coiled up in frothy, sometimes bloody exudate in the bronchi, alveoli and trachea. Lungs of heavily infected pigs were mottled with white, fibroid, scar-like tissues. The intestinal threadworm (Strongyloides sp.) was probably under-represented in samples taken because of its tendency to burrow into the intestinal walls.

Stephanurus dentatus was the least site specific and most tissue invasive internal parasite (Table 44). Among pigs parasitized, 38.2% were heavily infected. Adult worms were usually concentrated in the perirenal fat and adjacent tissues, but also were found in the pelvis of kidneys, inside ureters, and encysted in lumbar muscle and lung tissue of three pigs. Immature worms occurred in the liver, but adults were also recovered from abscessed sites. Livers of heavily parasitized (>50 adult parasites per host) pigs had large, diffused and generally protruded pus-filled or hemorrhagic abscesses, and fibrotic areas. Lesions were distinguishable from the much smaller and discrete lesions produced by the intestinal roundworm (Ascaris lumbricoides). Heavily parasitized pigs, despite extensive liver and kidney damage, appeared normal, indicating that the animals could withstand high parasite loads without becoming terminally ill.

Some parasites appear to be more prevalent in older individuals than in juveniles (Table 45). The hypothesis that parasite prevalence was independent of pig's age was rejected for A. lumbricoides ($P<0.05$) and S. dentatus ($P>0.005$). Percentage prevalence for A. lumbricoides

TABLE 45: Prevalence of nematode parasites in relation to age in 38 feral pigs in Kipahulu Valley.

Parasite	Percent prevalence				X^{2**}	Probability
	<1 year (8)*	1 year (7)	2 year (13)	3 year (10)		
Ascaris lumbricoides	37.5	71.4	30.7	10.0	7.92	$0.025 < P < 0.05$
Metastrongylus elongatus	75.0	100.0	92.3	90.0	2.71	$0.25 < P < 0.50$
Oesophagostomum sp.	62.5	85.7	61.5	60.0	5.34	$0.10 < P < 0.25$
Physocephalus sp.	0	14.2	8.3	10.0	2.37	$0.25 < P < 0.50$
Stephanurus dentatus	37.5	100.0	92.3	90.0	13.73	$0.001 < P < 0.005$
Strongyloides sp.	0	42.8	23.0	0	7.76	$0.05 < P < 0.10$
Trichuris suis	37.5	57.1	23.0	20.0	3.29	$0.25 < P < 0.50$

* Number of parasitised animals.

** Chi-square values were calculated using 2 x 4 contingency tables; df = 3.

was highest in one-year olds, but tended to decline with increasing age, due probably to some age-related mechanism of increased resistance to this parasite. Infection by S. dentatus was independent of age in animals greater than one year old ($X^2=0.72$, df=2, P>0.05), but was significantly lower in pigs less than one year than in all pigs older than a year ($X^2=9.64$, df=1, P>0.005). Thus, S. dentatus was a more important parasite in post-juvenile and adult pigs.

The following is a discussion of the possible effects the parasite fauna could have on feral pigs and why habitat factors were considered important for the maintenance of high parasite prevalence in the population.

None of the protozoan parasites are of pathogenic importance, but some coccidial parasites cause diarrhea in domestic pigs. Balantidim coli occurs naturally in pigs and may produce ulceration of the colon (Dunne & Leman 1975). This parasite thrives mainly on starchy food in the intestine and does not invade the intestinal epithelial cells so long as starchy foods are abundant (Chatterjee 1967).

Louse infection appeared to be affected by the pig's social behavior, body condition and coat density. Newborn piglets most probably acquired lice from their infected nursing mothers. Wallowing would help to reduce the ectoparasite, and social nesting would aid in the transmission of Hematopinus suis from one pig to another. Pigs in excellent nutritional condition were generally free of lice or lightly infested, as were animals with short hair and sparse coats. Pigs with a well-developed mane and a thick coat generally had moderate to heavy lice infections. Spinal hairs were the longest, thickest and densest on the body, and by virtue of their location were relatively less muddied, rubbed against or brushed by vegetation, compared to hairs on the flanks of the body. Hence, there is available to the parasite a greater length per hair filament for egg-laying. Moreover, eggs deposited on the spinal hairs are better protected against exposure and physical damage. These factors explain the variable intensity of lice infestation among the pigs. Heavy infestation produces skin irritation, blood loss, anemia, and can predispose animals to other sickness (Dunne & Leman 1975). Sarcoptes sp. appears to be an unimportant parasite in the rain forest. Giffin (1978) noted that mange parasites were more common in pig populations from dryer areas than in wet forests.

Helminth parasites frequently resulted in debilitation and death in domestic pigs. Larval migrations of A. lumbricoides produce lung and liver lesions, respiratory disturbance, pneumonia and hemorrhage. Adult worms occlude bile ducts. Whipworms (Trichuris suis) are embedded in the intestinal wall. Massive infections retard growth and produce hemorrhage and localized infections (Powers et al. 1960). Strongyloides sp. in domestic pigs are known to produce hemorrhage, anemia and diarrhea. The stomach worm, Physocephalus sp., commonly produces gastritis and stomach ulcerations. This parasite has a low prevalence and feral pigs were only lightly infected. Beetles (Scarabeidae and Aplodidae) are intermediate hosts for stomach worms (Zajicels & Pav

1972). Heavy infection by the nodular worm (*Oesophagosomum dentatum*) are known to produce weight loss, diarrhea and even death.

The kidney worm (*Stephanurus dentatus*) and lungworm (*Metastrongylus elongatus*) are the two most destructive and invasive nematode parasites in the study population. Similar results were obtained by Babero et al. (1959) and Giffin (1978) for feral populations parasitized with these two nematodes. Together, *Stephanurus dentatus* and *Metastrongylus elongatus* affected three vital organs--lung, liver and kidney--by producing abscesses, cysts and fibrous tissues. In domestic pigs, *Stephanurus dentatus* causes severe unthriftiness, occlusion of portal veins, hemorrhage, peritonitis, posterior paralysis and death (Alicata 1938; Dunne & Leman 1975). Posterior paralysis resulting from heavy *S. dentatus* infestation is reported also in feral pigs (Smith & Hawkes 1978), and in pen-reared wild boar (Henry & Conley 1970). Larval migrations of *Metastrongylus elongatus* through capillary walls produces severe petechial hemorrhage and adult worms cause respiratory disturbances, lung fibrosis, lung collapse, pneumonia and death (Alicata 1935). In some wild populations, lungworm parasitism is important to population mortality. The boar population in the Kampinos National Park, Poland, suffered weight loss and juvenile mortality because of metastrongylial parasitism (Fraczak 1974). In the Voroneshsky Reserve, Soviet Union, parasitism by lungworms and other helminth parasites contributed to the decline, especially during the winter, of the wild boar population (Ramashov 1977).

The high prevalence and intensity of nematode parasitism in this feral population can perhaps be attributed to climatic conditions, nematode-oligochaete associations and the pig's food habits. High rainfall, shade and the perpetually wet soils in rain forests favor the survival of free-living, infective larvae, particularly those of kidney worms, and the eggs of other helminthic parasites which are susceptible to dessication and exposure to direct sunlight (Alicata 1935). That the non-seasonal rain forest habitats are more conducive to helminth maintenance than the dryer, seasonal and more arid mountain pasture habitats is borne out in Giffin (1978). The prevalence of nematode infection in pig populations of rain forests was higher than for populations in mountain pasture habitats.

Over 14 species of earthworms can be naturally infected with metastrongylid larvae through their feeding on embryonated eggs in the droppings of infected pigs (Ivanova 1970; Poiner 1978). Earthworms were also known to host kidney worms (Soulsby 1965) and were suspected to be a mode of transmission in the feral population on Robert's Island, Canada. None of the nine species of earthworms collected from the pig's home ranges were examined for nematodes but several of these earthworms were probably naturally infected with metastrongyllids (Gates 1981 Florida - pers. comm.). At least four species of worms in this study were attracted by and fed on pig droppings. Field displacements of pig feces demonstrated a follow-the-feces movement in earthworms when droppings which had attracted worms were transplanted a few cm distance to a new site. As many as 50 or more earthworms would aggregate under a fecal dropping. Occurrence of earthworms over the entire Valley, abundance in wet forest soils and their availability as a year-round food item to pigs strongly suggest that metastrongyllid infection will be constantly maintained at a high level via the nematode-oligochaete paratenic association and pig-earthworm food chain. Ivanova (1980) observed that metastrongyllid infection in wild boar populations in the Pereslavl State Forest, Soviet Union, was dependent on earthworn abundance and its importance in the diet of the boar.

The absence of intestinal cestodes may be due to sample size, the perfunctory parasite explorations in some necropsies or diet. Ferns (Dryopteris sp.) contain the antihelminthic compound, filicin, which is effective against several intestinal cestodes (Chatterjee 1967). Giffin (1978), however, reported the occurrence of the cestode, Taenia hydatigena, in feral pigs on Hawaii. Some helminthic parasites pass their life cycles in intermediate hosts served by snails. Land snails (Succines sp., Bradybaenia bradybein) were observed feeding on fresh pig droppings, indicating that these mollusks could serve as intermediate hosts for free-living cestodes or perhaps other helminthic parasites that have escaped detection.

Parasites probably contribute to some losses from the population. Unlike predation, parasites do not kill pigs at infection, but gradually debilitate the animals through tissue damage. Necropsies showed pigs withstood heavy infestations without being terminally ill, thus indicating the high tolerance to parasitic infection. Stephanurus dentatus and Metastrongylus elongatus were considered to be the most harmful of all the helminthic parasites. Since infection was typically at a rate of more than two parasite species per pig, a compounded parasite load and more widespread damage at increased number of infective sites could weaken the animal's health considerably, lower its resistance to disease, and make it more vulnerable to secondary infection and unfavorable habitat factors. All age groups were susceptible to infection. Stephanurus dentatus was, however, more important in post-juvenile and adult populations probably because of the long period of prepatency (4 to 6 months) in this parasite (Soulby 1965) while Ascaris lumbricoides was important in the younger population. The forest soils and invertebrates that served as secondary hosts are constant sources of parasite infection for pigs. The availability of earthworms, nematode-oligochaete paratenic association and the importance of earthworms in the diets of feral pigs, collectively suggest that metastrongyllid and kidney worm infection will be maintained at a level of high prevalence, and that their contributions to mortality may be more significant than those of other helminths.

Dento-alveolar Diseases

In many dentate mammals, the loss of teeth could severely impair feeding capabilitites and predispose affected animals to malnutrition, starvation or death. The frequency of tooth loss in wild pig populations is unknown (Hall 1945). Feral populations in California had a high incidence of missing teeth during old age and progressive tooth loss was thought to be a source of adult mortality (Barrett 1978).

Lower jaws of 53 trapped and shot pigs and 15 hunter-killed pigs were aged and the condition of the teeth examined. Fourteen jaws were radiographed to examine diseased teeth and surrounding bone structures.

Three processes were observed to contribute to the breakdown of dentition and their associated structures: 1) attrition (tooth wear resulting from mastication of fibrous or granular food), 2) erosion (loss of tooth structure by chemical action, usually acids), and 3) dento-alveolar disease. Erosion of teeth was evidenced by the presence of scooped-out dentinal depressions (cupping) in the occlusal surfaces, and was considered to be a more rapid process of tooth structure loss than normal attrition. Pigs with dento-alveolar disease had one or several of the following: caries, periodontal pockets, bone cavitations, abscesses or other jaw diseases.

The extent of age-related tooth loss was studied by scoring, for each lower jaw, the number of teeth with dento-alveolar disease (D), cupping (C) or missing (M) teeth. Each affected tooth was scored once only. Missing teeth included absent and nonfunctional (attrited to the roots) teeth. The number of diseased, cupped or missing teeth (DCM) per 100 erupted mandibular permanent teeth was calculated. Total DCM teeth was calculated as the sum total of D, C and M teeth per 100 permanent teeth. The average number of DCM teeth per year class was obtained by dividing DCM teeth by the year class sample size.

From a total of 263 affected teeth in 68 lower jaws, the percent composition of DCM teeth were: 32.6% with dento-alveolar disease, 29.9%

attrited and eroded, and 38.2% missing teeth (Table 46). Pigs less than one year old were relatively free of dental problems. Less than 10% of the erupted teeth were diseased, eroded or missing (DCM teeth <1). The youngest animal with dento-alveolar disease and missing teeth was aged at 6 months. Percent DCM teeth, however, increased progressively with age (Figure 36). One-year olds averaged nearly two DCM teeth per animal, three-year olds about four and four-year olds more than six DCM teeth.

Although DCM index increased progressively with age, certain breakdown processes were more characteristic of particular age classes. Molar cupping, important during the first three years but not in old age, contributed more than either diseased or missing teeth to the total DCM index. Cupped teeth in two-year olds averaged higher than diseased or absent teeth. Dento-alveolar disease was important in older animals. There was more than a threefold increase in the average number of diseased teeth between the ages of two and three years. Four-year olds averaged more than four diseased teeth per lower jaw. Diseases of the alveolar bone appeared to be less prevalent when most of the posterior teeth had been lost, as in the case of older animals. Missing teeth were important after the fourth year. Five-year olds averaged 12 missing teeth per lower jaw, which is equivalent to a loss of 53.7% of the permanent dentition.

Tooth loss was observed to be principally due to dento-alveolar diseases and attrition erosion rather than to caries. Horizontal impaction of the third molar, especially when partially erupted, also

TABLE 46: Age related prevalence of diseased, cupped or missing permanent teeth per lower jaw in 68 feral pigs in Kipahulu Valley.

Age (year)	Number of mandibles (N)	Number of permanent mandibular teeth	Average number of affected teeth*			
			Diseased teeth (D)	Cupped teeth (C)	Missing teeth (M)	Total DCM teeth***
<1	10	96	0.10 (1)**	0.60 (6)	0.20 (2)	0.90 (9)
1	14	246	0.42 (6)	1.28 (18)	0.21 (3)	1.92 (27)
2	18	396	0.77 (14)	2.11 (38)	0.61 (11)	3.50 (63)
3	11	242	2.63 (29)	0.72 (8)	0.45 (5)	3.80 (42)
4	8	176	4.12 (33)	0.87 (7)	1.37 (11)	6.37 (51)
5	6	132	0.50 (3)	0 (0)	11.33 (68)	11.80 (71)

* Calculated as the number of diseased, cupped or missing teeth divided by N.

** Number of affected teeth.

*** Calculated as the total number of affected teeth divided by N.

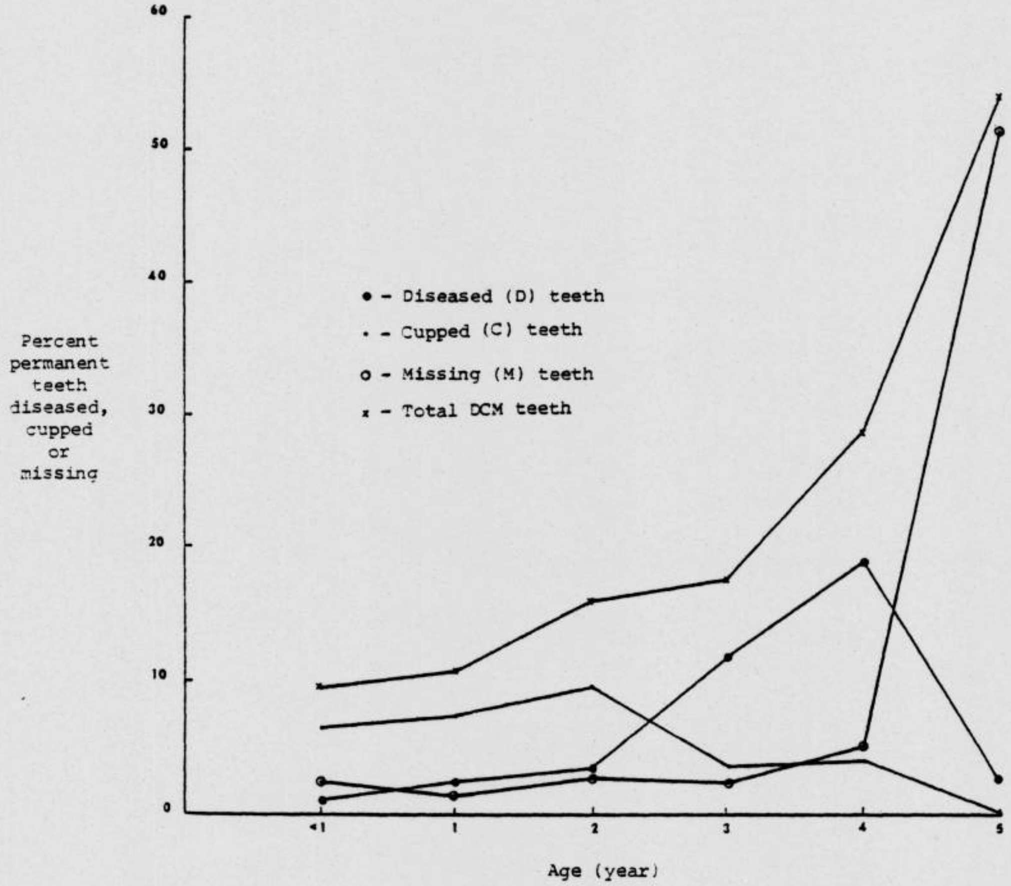


Figure 36: Prevalence of diseased, cupped or missing teeth in erupted permanent mandibular teeth in 68 feral pigs in Kipahulu Valley.

has the potential of causing caries to form on the distal surface of the second molar mesial to it. The carious lesion may progress to more severe dento-alveolar disease and predispose the second molars to be exfoliated. Alveolar disease generally took the form of gum recession, loosening of teeth through bony pockets in alveolar bone or abscesses (cavitations in the basal bone). Alveolar disease was thus commonly accompanied by loss of bone tissue. In advanced disease conditions one or more roots were exposed and diseased teeth were sometimes extruded (islanded) above the occlusal plane of the surrounding teeth. Diseased teeth were, however, more commonly broken down until they did not contact opposing teeth. In a severe case of dento-alveolar disease, an open tract had developed from the abscess to drain pus from the diseased site. The diseased tooth was not only lost, but a vertical perforation of the mandible from the occlusal aspect to the lower rim of the mandible, accompanied by bony thickening, resulted. Vertical alveolar bone loss appeared to be irreplaceable, whereas bone loss due to abscesses was remarkably replaceable in cases where the tooth exfoliated. Bony swelling in the mandible of one animal could be due to abnormal bone development, cystic lesion, carcinoma or some other bone disease initiated by dento-alveolar abscess.

The dentition showed varying susceptibility to dento-alveolar disease and tooth loss. Molars were more disease-prone than premolars or incisors. The first molars were generally the first teeth to be diseased, eroded or lost, and as early as at eight months old. The second and third molars appeared to be equally disease-prone and were generally attrited and lost together. Third molars in a few animals were diseased and attrited before the second molars and somewhat peculiarly from the distal to the mesial aspects of the teeth. The sequence of tooth loss as revealed from the sample population was: M1 to M23 to P4321. If pigs could still survive for long, which is improbable, after being partially edentulous with the loss of the molars and premolars, then the incisors would be the next set of teeth to be exfoliated leaving only the canines which have no feeding capabilities.

Although the molars were highly fissured with deep fossae, pitted and hence, caries prone, the prevalence of caries was low. Occlusal surfaces were less susceptible to caries than the mesial, distal, buccal or lingual surfaces. Interproximal caries at the distal and mesial surfaces of M1 and M2, respectively, were observed to be initiated by food impaction and improper interdigitation of the larger proximal cusps of the opposing maxillary first molar with the mandibular M12. The low caries prevalence may be for two reasons. Pits were probably attrited faster than caries initiation and progression. Diets consisting mainly of plant matter might have reduced onset of caries because chlorophyll is known to possess anticariogenic properties.

Dento-alveolar diseases and tooth loss invariably reduce longevity and are considered important sources of adult mortality. Diseased teeth involving the alveolar bone may produce localized or systemic infection and predispose the animal to death. Barrett (1978) wrote: "if large (teeth) abscesses contaminate the blood, the animal may die of a generalized septicemia." Although radiographic examinations showed that basal bones lost in association with tooth diseases could be replaced, more severe dento-alveolar disease always led to bone cavitations and irreplaceable vertical alveolar bone loss. Bone loss is particularly insidious because it weakens support which could loosen and exfoliate unaffected teeth, thus hastening further loss of teeth and their alveolar structures.

Sows with severe tooth loss and consequent feeding impairment are unlikely to raise a healthy litter, even though they may still be fecund. Boars with severe teeth problems may be more withdrawn and less successful than those with healthy teeth for mates during mating contests. Thus, tooth problems could indirectly reduce animal numbers by curtailing productivity via certain forced behavior patterns.

As in parasite infection, feral pigs seemed to show a high resiliency to dento-alveolar disease and could survive a loss of over 50% of their dentition. This conclusion is, however, somewhat biased because the sample population consisted only of surviving animals.

Tooth loss is cumulative, permanent and irreversible. As teeth are being lost, the pig is gradually deprived of its feeding apparatus and masticatory surfaces. Food intake may be reduced and feeding habits may be modified. Stomach capacity may decrease. Diets involving a switch to softer foods, or foods which can be swallowed without much mastication, may be necessary. Pigs partially edentulous with loss of their molars and premolars are unlikely to be able to feed effectively on such common foods as tree fern, ieie, tree bark or graminids.

Impairment of feeding capabilities resulting from dento-alveolar disease and teeth loss was evident. In several diseased jaws with unilateral tooth deficiencies, the teeth on the diseased side had matted surfaces, were heavily stained and lacked the shine compared to teeth on the other side, indicating that the animal was probably not using the diseased tooth row for mastication. Such reduced feeding capability and resultant diet modification could cause malnutrition and predispose such animals to other diseases or death.

Other Diseases

Feral pigs on the island of Hawaii are hosts to several infectious diseases (Giffin 1978, 1981). The presence of Brucella or Leptospira organisms in this feral population was studied by serological methods.

With the standard card test (Buffered Brucella Antigen Test), 20 serum samples that were tested for antibodies to Brucella yielded negative results. Serological tests for Leptospira using Fort Dodge antigen against serotypes L. icterohemorrhagiae, L. pomona, L. grippotyphosa and L. hardjo were all negative. Low background titers of 1:10, for serotypes L. pomona, and L. canicola and L. icterohemorrhagiae were recorded from two and three animals, respectively. Test results were significant only when titer readings exceeded 1:50.

Feral Dog Predation

The presence of feral dogs was established early in this study. Scats that looked unfamiliar but belonging to a carnivore were sent to

Dr. P. Q. Tomich, who identified them as typical of dog droppings found in forested areas throughout the Hawaiian islands.

Predation by dogs on feral pigs was observed once only on February 10, 1980, at about 300m west of E880m. The sighting involved two adult dogs (one black and another grayish) cooperatively attacking a year-old sow. One dog, upon sensing my presence, stopped biting the sow and approached me, while the other continued with its attack. The approaching dog was shot, whereupon the other fled. Stomach contents consisted of remains of a whole rat, fresh blood, few pig hairs and traces of Hilo grass (Paspalum conjugatum). The sow sat sprawled on the ground. Large amounts of muscle had been bitten away, and the femur of one leg and the scapula on the other side of its body protruded outwards. Numerous accounts of feral dog predation on pigs and feral mammals have been documented (Tomich 1969). However, the predator-prey relationship between the dog and pig remains unclear and appears to be unimportant at the present time. Dogs, excepting the above observation, were never seen although they were heard several times in the night and during the day. They occurred in low numbers; their free-ranging habits were clearly evidenced from the droppings seen on the trails, sedges and grassy flats. Each of 34 dog scats collected from 610 to 1525m over a 20-month period contained rat remains, probably all from the roof rat (Rattus rattus). Feral dogs in rain forest habitats on the island of Hawaii subsist largely on roof rats (Tomich 1969; Mueller-Dombois et al. 1981). Thus, the carnivore niche of feral dogs appears to be provided principally by rats rather than pigs.

Mongoose Predation

During this study attempts were made to follow up on squeals or distress sounds made by pigs. These pursuits led to observations on dog predation, sows nursing piglets, pigs in play, foraging and shelter-use behaviors.

Pursuit of a continuous, piercing piglet squeal heard at 1630 on May 12, 1980, about 50m west from K2500 resulted in a surprising observatin of a mongoose attacking a stray piglet. The mongoose had seized the piglet at its throat and stubbornly held on to its bite throughout the attack. The piglet remained in a standing position, moving its head up and down and sideways as if to shake loose the predator. Since the mongoose was longer than the distance of the piglet's neck above the ground, it was not lifted off the ground by upward head movements of its prey. Instead, both its hind legs were firmly planted on the ground. Struggle by the mongoose was more vigorous than the piglet. Mongoose attack strategy consisted of repeated clockwise and counterclockwise head twisting about the bite wound, violent lateral body movements and tail whipping on the ground. Occasionally, the mongoose would thrust its head upwards, hence biting deeper into the inflicted wound.

Both mongoose and piglet rolled over twice down the ridge slope. Upon sensing my presence, the mongoose momentarily ignored the squealing piglet, stood upright on its hind legs and with head levelled, maintained a very brief curious gaze before fleeing into a ground hole at the base of a koa tree five meters away from the first-observed attack site. When the mongoose did not appear after five minutes, the piglet was handcaught for examination. Bleeding was profuse from the deep puncture wounds, and was the most likely cause of death four hours later in captivity. The piglet, two weeks old, weighed five pounds while the weight of the mongoose was estimated from captured similar-sized animals to be about 1.5 pounds. Thus, the mongoose attempted to take a food three times greater than its own size.

Subsequent to this observation, seven Tomahawk (Nasco, California) traps were set up from 610 to 1450m. Traps were baited with either canned tuna or chicken bones. Eighteen mongooses and five rats were captured from an expenditure of 75 trap nights. Mongooses were caught as high as 1450m. Necropsies revealed pig meat and hairs in five stomachs. Unfortunately, mongoose trapping was conducted during a period when trapped and shot pigs were necropsied for parasite survey and food habits studies. Hence, it was not possible to establish whether pig meat in the stomachs was derived from direct predation. The mongoose was the most noticeable animal at sites of trapped pigs and was frequently observed to feed on pig carcasses shortly after necropsies were performed.

CHAPTER 12

MANAGEMENT

Introduction

The National Park Service (NPS) was created in 1916 to preserve native biota. Over the years, NPS policy has matured to that of purposeful management of plant and animal communities for preserving biological resources. Whenever exotic plants or animals threaten the protection or interpretation of natural resources being preserved in a park, this agency manipulates, within policy, political and legislative constraints, the numbers of such species using control and eradication methods.

The shift in management practice from preservation of species population(s) to purposeful management of whole habitats is consistent with modern ecological findings. Haber (1974) emphasized the need to manage natural areas as a whole, rather than as parts or separate entities. In the Hawaiian Islands, the U.S. Fish and Wildlife Service has also shown that the perpetuation of native species populations is dependent on the preservation of their whole habitats.

At Kipahulu Valley in Haleakala National Park (hereinafter referred to as the Park) the manager's primary focus is the maintenance of the rain forest ecosystem in its natural state. This holistic management perspective is necessary to ensure that natural ecological processes and complex community interrelationships are preserved intact. Only with this management framework can the Park ensure that this upland rain forest will continue to function as a pristine Hawaiian wildland refuge for its native biota.

The feral pig issue becomes pertinent to the Park's management program only when it interferes with the Park's above-mentioned goal. Hitherto no specific information has been available to the Park manager to define the nature or extent of the pig problem. Consequently, there has been no control program. This was despite the following recommendations by earlier parties who observed "serious damage," and disruptive effects of pigs to this natural reserve:

1) "...immediate steps should be taken to reduce or eliminate the wild pig population within this Valley, by any suitable means." Warner 1967: p. 8.

2) "...special efforts should be made as soon as possible to drastically reduce the number of pigs in this area, if not to eliminate them completely." Lamoureux & Stemmermann 1976: p. 10.

In evaluating its management program in Kipahulu Valley, the Park should ask: Is a management decision necessary? A decision presupposes the existence of a problem. Thus, the reassessment of this resource question requires a comprehensive understanding of the feral pig problem. This management report begins by considering three interrelated questions:

1) What is/is not the feral pig problem in Kipahulu Valley?

2) What are the consequences for doing nothing?

3) Why control feral pigs?

Is a Managment Decision Necessary?

(a) Nature of the feral pig problem

(i) Dispersal agent for the strawberry guava, Psidium cattleianum.—Feral pigs actively disperse the strawberry guava for six months of the year by feeding on the fruits and carrying large quantities of seeds undamaged in their digestive tracts. Gut transport did not lower seed viability, but speeded the germination rates (Chapter 7).

(ii) Reduction in abundance of native trees and herbaceous plants.—Feral pigs direct their feeding pressures at no less than 40 plant species, 75% of which are natives in the herbaceous-subcanopy understory, and of these 85.7% are endemics. Several of these species are major components of the ecosystem. Native tree ferns are a staple of the pigs' diet. These trees are either felled and troughed or vertically troughed to obtain their starches and sugars. Bark feeding directly kills several species of native trees (Chapter 6).

(iii) Disruption in forest subcanopy.—Tree ferns provide a special spatial dimension in the koa-ohia forest in that native trees are often epiphytic on them. Felling of tree ferns by pigs brings a substantial cover loss. Disruption to forest structure is evidenced by changes in forest floor species composition favoring exotics (Chapter 6).

(iv) Establishment of weedy species.—Pigs create seed beds for the establishment of several weedy species by their rooting activities. A more than threefold increase in the number of exotic plant species from 1945 to the present time can largely be attributed to increased pig activities (Chapters 3, 4, 6).

(v) Soil erosion.—Pigs initiate soil erosion by breaking the ground cover to root for earthworms. High rainfall promotes loss of top soil, particularly from frequently rooted sites. The production and heavy use of trails by pigs in some areas initiate gully erosion and produce localized changes in ground topography (Chapter 6).

(vi) Increase in the number of sites of standing water.—Wallows and troughed out tree fern trunks capture and hold rain water and thus increase the number of available breeding sites for *Culex pipiens*, a vector for avian malaria. Standing water in tree fern trunks appears to be superior over those in wallows as breeding sites, apparently because of its elevation from the ground (Chapter 6).

(b) The consequences of doing nothing

(i) Replacement of native forest formation by the exotic strawberry guava.—The pig-strawberry guava-tree fern association (Chapter 6) threatens to displace the native tree fern forest with the strawberry guava. Pigs increase the standing crop of strawberry guava by dispersing essentially undamaged seeds, thus maintaining an open food chain with it. The temporal dimension in the pig-strawberry guava synergistic relationship is exemplified by the fact that pig-aided dispersal of the guava accelerates the spread of this shade tolerant tree into new areas under the forest canopy. Island ecosystem studies in Hawaii have shown that the strawberry guava is an active invader in rain forests and damages native ecosystems by forming solid stands which successfully outcompete native plants (Mueller-Dombois et al. 1981).

(ii) Increase in exotic species pool.—The exotic species pool in Kipahulu Valley will continue to increase with continued pig activity (Yoshinaga 1980). Elsewhere in the Hawaiian Islands, feral pig activities have been reported to alter the species composition of native ecosystems and replace them with grassy and weedy formations (Chapter 6).

(iii) Loss of native plants.—Selective food habits and continuous grazing pressure on native plants over a relatively small home range area can progressively reduce or virtually eliminate some species populations. Marratia douglasii is found mostly in sites less accessible to pigs. Scarcity of this fern and other lobeliads is most likely due to pig activity. Local extinction of native plants resulting from feral pig or boar activities has been documented in New Zealand and Tennessee (Chapter 6).

(iv) Impact on native stream biota.—Pig rooting and erosion will undoubtedly increase the siltation load in streams and affect stream biota.

(v) Reduced recreational quality at Oheo.—Oheo

is a popular swimming ground for Park visitors. Pig activity could contaminate stream water and reduce its quality for recreational purposes.

(c) Reasons for initiating feral pig control

Feral pig control will:

1) prevent the undesirable consequences (as listed above) from happening.
2) restore the rain forest to its pristine condition.
3) preserve the rain forest ecosystem as a whole for the self-perpetuation of native biota.
4) ensure that the Valley will function as a refuge for its largely native and endangered biota.
5) maintain the Valley as a natural wildland laboratory for the study of natural ecological processes.

6) carry out the goals for which the Park is commissioned to do.

7) maintain the forest in pre-Hawaiian or Hawaiian status.

(d) Present management practice

Hitherto the Park's policy on the feral pig issue may be termed as one of passive management. Natural and disruptive events are allowed to run their courses. Hunting in the upper pastureland, Palikea and lower plateau probably has a depressing effect on the population. Park records on hunting activity are too scanty for any management interpretation.

(e) The management decision

From (a) and (b), it is evident that a management decision is necessary. An affirmative answer cannot be given to this resource managment question: Can the rain forest be preserved in its natural state by passive management? The consequences of not acting on the pig problem are the disruption deterioration and destruction of the native habitat through displacement by the strawberry guava and other weedy species. Native biota will be threatened as their habitats are disrupted. It is recommended that the Park initiate a feral pig control program. This decision is necessary to avoid or prevent the undesirable consequences (as listed above) from occurring and to reduce, narrow and stop the pig threat.

Management Goals and Objectives

The formulation of control objectives and policies must come from the Park itself. No other agency has the same concerns or habitat management policies as NPS. It will be desirable for the Park's research body, the CPSU (Cooperative National Park Resources Studies Unit), to assist in the formulation, analysis and periodic evaluation of control objectives.

The goals of feral pig control should be: (1) to free Kipahulu Valley of feral pigs, (2) to prevent it from reinvasion by pigs in any of their states of existence, and (3) to effectively maintain the Valley pig free.

Control objectives should be realistic, measurable and flexible, bearing in mind the following constraints: terrain, fragility of the ecosystem and limited control technology applicable to the area. The objective "to eradicate feral pigs" is unrealistic, initially. The verbs such as "eradicate," "eliminate," "depopulate," "exterminate" or "extinguish" mean essentially the same thing in this context, but connote, as was borne out from interviews in the Hana district, an abrupt deprivation of a meat resource, loss of a recently developed hunting tradition and the spectre of danger from poisons used against pigs. These control verbs should probably not be used until the latter part of the control program. For instance, when control operations have lowered the number of pigs in the Valley to 30 or fewer, then the control objective "to eradicate" will be more appropriate for the remnant population. It should be stressed that feral pig control must have a built-in eradication objective in order to be worthwhile. Otherwise control efforts will only increase population variance.

It is recommended that control objectives be formulated on a term basis as follows:

1) short term objective: to reduce the pig population to a predetermined low level, temporarily acceptable to the Park.
2) intermediate term objective: to stabilize the population at the regulated low level. If the Park accepts the threshold tolerance to pigs, then the need for further control operations depends on whether the population density remains below or above the threshold level.
3) long term objective: to eradicate remaining animals from the management unit.

Criteria for Selection of Control Methods

The Park manager has little information on the possible effects of control technology and operations on habitats like Kipahulu Valley. For this reason, it will be desirable for the Park to weigh decisions on control operations against two sets of criteria, the absolute and the essential. These criteria should function to protect the habitat and to act as a safety factor for what is not known about the effects of control operations on fragile rain forest habitats. Absolute criteria for control operations, for instance, could be minimum habitat impact, non-environmentally polluting and effectiveness in directly reducing pigs. The Park's guidelines for research activities in ecologically sensitive areas are in need of some revision, but can be used as an aid to formulate these criteria for pig control.

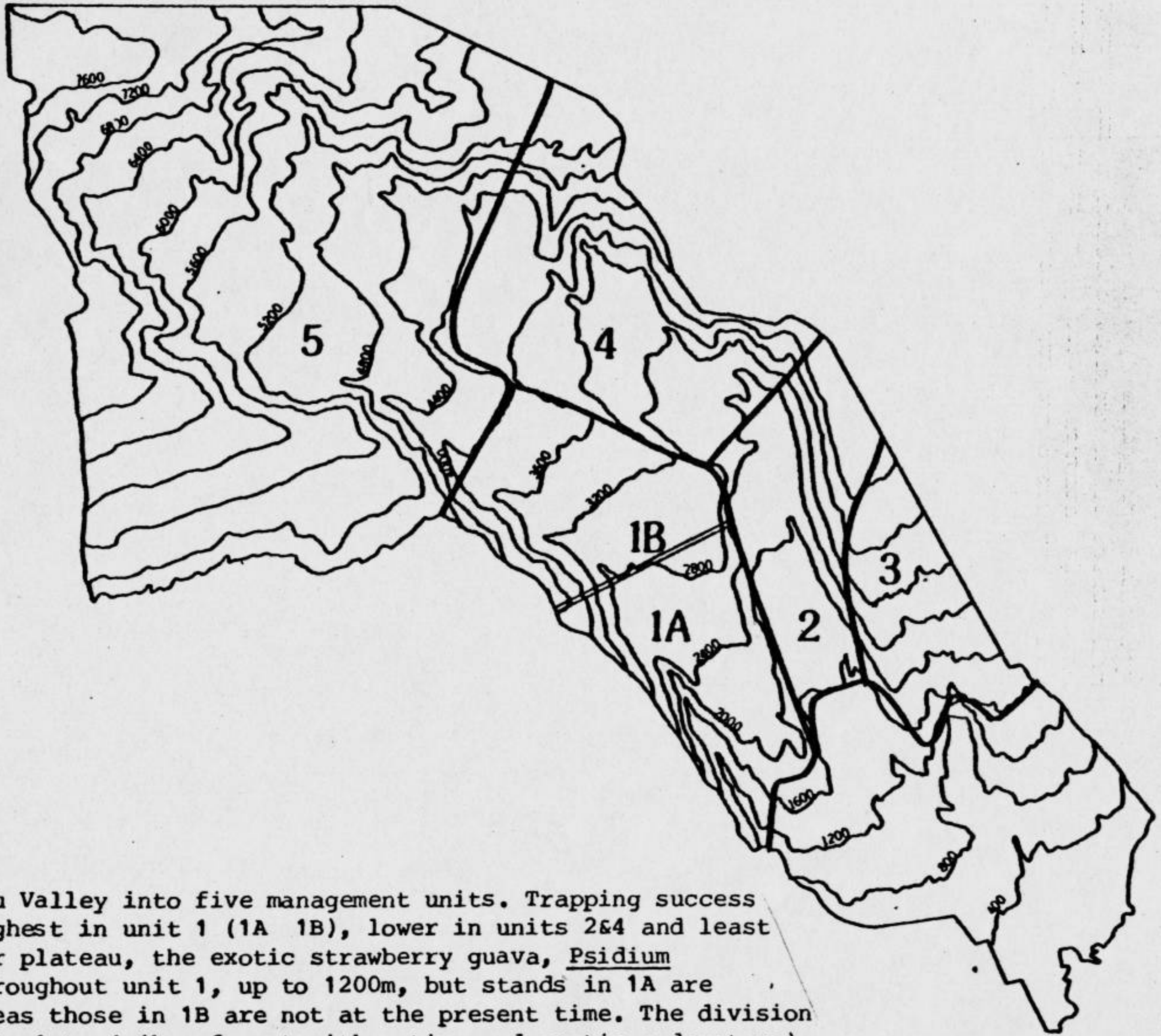
Management Units

Over what area should the control be undertaken? The Park should adopt an incremental approach for direct reduction and concentrate its efforts first on the most impacted area. The Valley can be subdivided into five management units using the information on population density, trappability index, movement patterns, distribution of the strawberry guava and other logistical considerations (Figure 37). This subdivision indicates management priorities. Thus, unit 1 has highest control priority (1A>1B), and the maintenance of stabilized low density in unit 2 will be dependent on management activities for unit 3. Division of unit 1 into two subunits, 1A and 1B, is ecological and takes into consideration the fact that strawberry guava stands in 1A are self-maintaining, whereas those in 1B are not. Stratification of the Valley into management units will assist the manager in deciding the appropriate management tools for each unit and at the same time allow him to use the results of control operations in one unit to another.

Strategies

During the planning phase of the control program, it will be desirable to explore ways of increasing the vulnerability of the population to various control efforts. Control functions should be

Figure 37: Subdivision of Kipahulu Valley into five management units. Trapping success and pig density are highest in unit 1 (1A 1B), lower in units 2&4 and least in unit 5. On the upper plateau, the exotic strawberry guava, <u>Psidium cattleianum</u>, occurs throughout unit 1, up to 1200m, but stands in 1A are self-maintaining, whereas those in 1B are not at the present time. The division of the Valley into units 1 to 4 (koa forest with native and exotic understory) and 5 (ohia forest with native understory) follows the vegetation map of Jacobi (Chapter, Figure 10). Management options for each of the five units are shown in Table 48.



Subdivision of Kipahulu Valley into five management units. Trapping success and pig density are highest in unit 1 (1A 1B), lower in units 2&4 and least in unit 5. On the upper plateau, the exotic strawberry guava, Psidium cattleianum, occurs throughout unit 1, up to 1200m, but stands in 1A are self-maintaining, whereas those in 1B are not at the present time. The division of the Valley into units 1 to 4 (koa forest with native and exotic understory) and 5 (ohia forest with native understory) follows the vegetation map of Jacobi (Chapter, Figure 10). Management options for each of the five units are shown in Table 48.

aimed at destabilizing the population. This can be achieved by simultaneously removing animals from the top of the age structure using live-trapping, shooting and hunting (Units 2 and 3), and from the bottom of the age structure by systematic dogging. To reach the intermediate term objective, emphasis should be placed on the combined removal of young and older animals and to impact entire groups. Tipton (1980) estimates that the stabilized low level can be achieved by cropping 40% of the older age class and 60% of the younger age class.

All management activity using nonchemical or chemical control technology should be targeted at whole groups rather than individual animals. The senses of smell and hearing that regulate group type formation and social behavior should be maximally exploited in baiting programs and in control research.

Control operations can be made to overlap periods when the population is most vulnerable. Unfortunately, vulnerability peaks were not clearly evident because breeding was continuous. However, based on gestation length and the minimum interval between breeding, it will be desirable to implement a 4 month-2 month recess-4 month control cycle to maximally impact the population.

Using the longevity estimate for this population (Chapter 11), 12 control cycles will thus be necessary if one pig in a cohort escapes being caught by any of the control methods. Theoretically, this will entail 48 months of management activity over 6 years. Given the small size of the management units and the total area, it might be possible to reach the short term objective for units 1, 2 and 4 in 2 years, with an expenditure of two consecutive control cycles per management unit. Should the Park decide to accept a feral pig threshold tolerance, it will be desirable to maintain and monitor the regulated stabilized low density (intermediate term objective) for at least one-half a cohort's life span.

Control Methodologies

(a) Available management tools

Pig control technology is still in its infancy. New methods can be expected in the near future. Currently used methods of control are: (1) physical--trapping, hunting, shooting, fencing; (2) chemical--poisoning, explosives; and (3) biological--disease, habitat manipulation.

Habitat manipulation is the most effective method of manipulating populations (Caughley 1977), but is inappropriate in this habitat. Disease (hog cholera) was used in Pakistan to control boar populations (National Research Council 1979). In parts of Europe, boar populations are reduced by 70-90% as a result of regular outbreaks of hog cholera (Pusch 1946). Outbreak of this disease in an off-shore island in California eliminated a feral population (Wiewandt 1977). Transmissibility of the virus between pigs in any state of existence is high, and an inoculation of one pig with the virus will suffice to introduce the disease into a population. The USDA will never approve this virus as a control agent (Garner & Matschke 1981). No consideration should be given to other exotic infectious agents for pig control as this conflicts with NPS goals and is tantamount to the agency "preaching water and drinking wine."

(b) Recommended management tools

(i) Trapping.—Live-trapping should be a major management tool. Once traps are baited, they are in continuous function until animals are caught. Operationally, trapping is the antithesis of hunting. Animals are sought out during hunting, but in trapping the desired goal is to make it easy for animals to seek out the traps. In high density areas, as in Unit 1, trapping can be expected to be efficient. Reduction by trapping has high public acceptability because of visible results and because the trapped pigs are available as food.

Whereas live-trapping is recommended in the low elevation units, kill-trapping would be a more practical management goal in Unit 5. Because of shorter survival period of trapped animals at this elevation and lower rate of trapping success (Chapter 8), the utilitarian aspect of this management tool is impractical. It is recommended that the Park experiment with foods with bait-life up to or in excess of 2 weeks. In the interim, impacted tree fern trunks and possibly potatoes can be used. A foot-long tree trunk halved for the first fortnightly baiting can be halved again at the second fortnightly rebaiting, thus giving the initial food bait a bait-life of one month.

Effectiveness of live-trapping depends on the following factors: trap design, location, number of traps and attractiveness of the bait. Metal box traps (Diong 1980) proved effective for single and multiple captures. Chain-link fabric can be attached to the door and rear panels to prevent piglets from squeezing out of traps. Corral traps are troublesome to maintain, impact habitat and are not escape-proof. Snares are potentially powerful control tools, but are difficult to set in selected sites without supporting materials. Kill-snares that do not require baiting should be explored for positioning along established or new trails. These snares can act as a supplementary tool during "mopping-up" operations. Because snares are dangerous to humans, control teams must be knowledgeable on their use and location in the field.

Number of traps is an important determinant of trapping success when they cannot be easily moved about. Based on diel home range areas, the minimum number of traps for maximum trap exposure in Kipahulu Valley is 35, 12 less than the total number of existing traps. Management alternatives can compensate for fewer traps if this is found to be the case in a unit; this the Park must explore.

Existing traps are located on the periphery of the animals' home ranges. To increase trapping success, it will be desirable to site traps near the animals' centers of activity. The center of activity line on the upper plateau runs approximately midway between the two existing trap lines. Catchability has been dependent on lateral movements from the interior to the edges of the plateau, and the distances moved up or down a trap line. Trapping opportunities for pigs in the interior of the plateau should be increased. The following alternatives exist: (1) move escarpment trap line to the interior; (2) maintain existing traplines, but add an additional one midway between the two; or (3) maintain existing trap lines, but add two traverse-plateau trap lines (Figure 38).

If a decision matrix is generated and rating values attached to a set of absolute and essential criteria, it can be shown from rating scores that alternative (3) is the best choice. Transverse trap lines X, Y, should serve to intercept uphill-downhill movements in unit 1A and between 1B and 1A. It should also be noted that total length for X and Y is less than in alternative (2). The management significance of transverse trap line Y will become apparent later.

The cost of a live-trapping program can be reduced, but at some expense in effectiveness, if the interval between baiting to inspection is increased. In the first half of the first control cycle, it is recommended that traps be inspected at a 3-day interval, thus totalling 60 inspection trips per one-half of a control cycle. Subsequently, depending on the density level and activity at previous baiting, inspection can be done 4 to 6 days apart, with no loss in the food value of trapped animals.

Attempts to demonstrate the feasibility of self-baiting traps were unsuccessful. Live baits, i.e., an estrus sow or one artificially

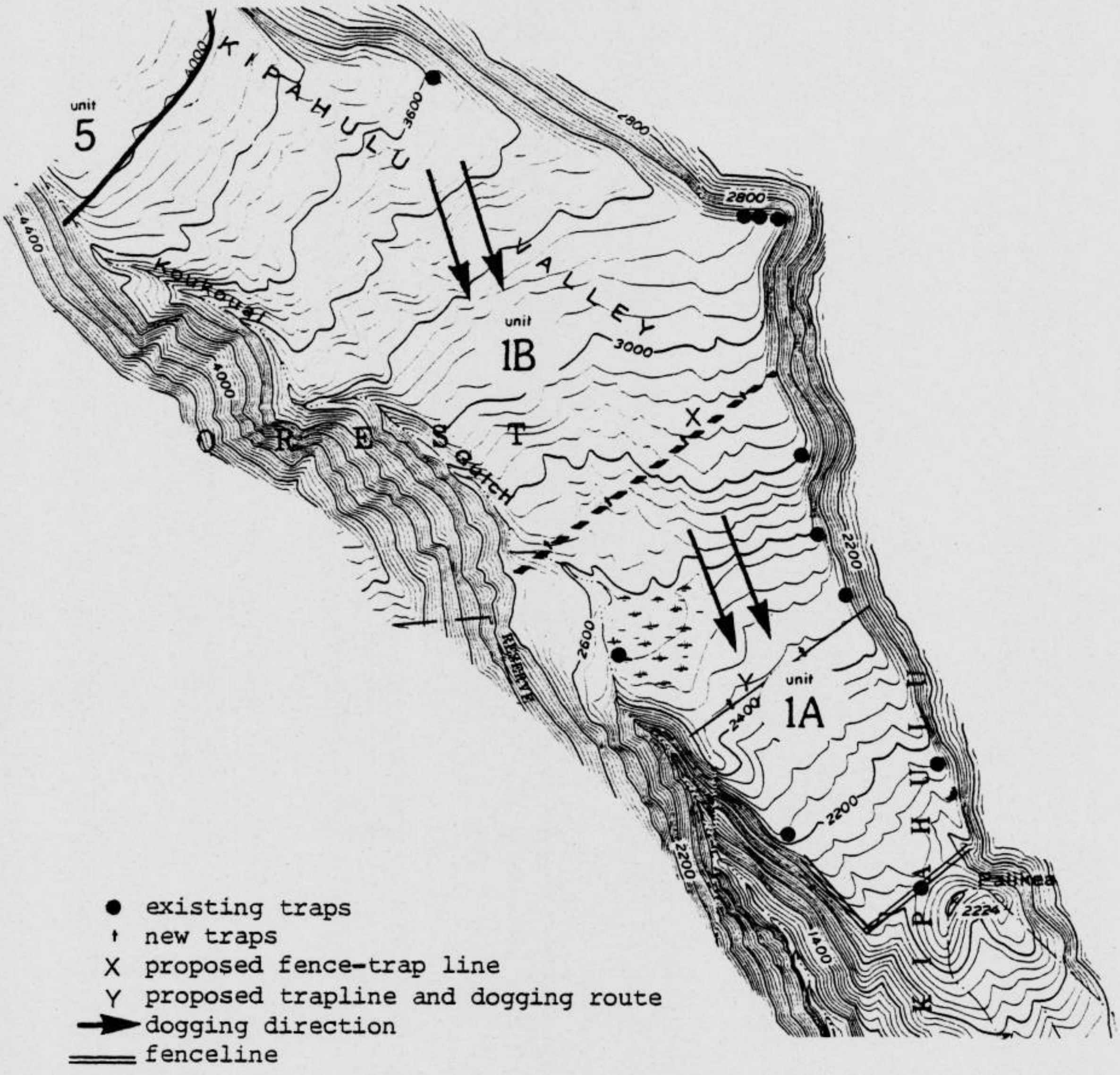


Figure 38: Proposed livetrapping and fencing activities for management **subunits** 1A and 1B. Fenceline X should incorporate the management objectives and activities illustrated in Figure 39.

induced, have considerable potential in attracting other animals and deserve experimentation.

Starchy foods that are bulky, possessing a long bait life (sweet potato) and with few nuisance problems are strongly recommended over loose, grainy foods for baits. Since the proximate fractions (NFE) in potatoes (Ripperton 1942) approximate very closely that of tree fern core (Chapter 6), potatoes should be readily accepted by the pigs. Elsewhere, potatoes and another tuber, cassava, are staple foods and baits for free-ranging pigs in Europe and the Far East. Potato farms in many agricultural areas are frequently invaded by wild and feral pigs. In Italy, dynamite was inserted in potatoes to control the Italian wild boar from agricultural areas. Potatoes and tree fern core, if desired, can be inoculated with toxicants using procedures illustrated by Diong (1980). Impacted tree ferns, whenever encountered, can be stored above the ground for subsequent baiting.

Because baits will have to be airlifted or backpacked into management units, it is recommended that the Park explore the possibility of ensuring a sustained supply of baits from within the Valley. Potato plots can be maintained on raised beds in the already impacted soils near Palikea saddle. Sugar cane is another plant suitable for this purpose.

(ii) Shooting and dogging.—Shooting is distinguished from hunting as the purposeful killing of all animals on sight regardless of their age. Dogging is the technique of flushing a predetermined area with a team of dogs and allowing the dogs to kill the pigs. Those pigs sighted during this process are shot.

Dogs were disallowed in this study because of Park regulations. Teams of dogs have, however, been effectively used in research and control of wild and feral pig populations in Hawaii (Giffin 1978); South Carolina; Cumberland Island National Seashore, Ossabaw Island, Georgia; Mississippi; Tennessee (Singer 1980 Gatlinburg, Tennessee - pers. comm.) and Malesia (Diong 1973). Dogging and shooting during the statewide Feral Pig Eradication Program, 1910-1958, was reported to be locally effective for reducing pigs in densely vegetated areas (Chapter 2). Giffin (1978) reported great success in catching and censusing pigs with catch and bay dogs in rain forests on the island of Hawaii. In difficult terrain, dogging has been shown to be many times more effective than drive hunting with rifle alone or with conventional trapping methods. When the Great Smokey Mountains National Park in 1978 decided to control the boar by professional dogging techniques, local hunters protested to halt the "experiment." Hunters testify that they know too well that dogs kill and impact the boar population better than any of the other control tools in use. Saywell (1943) and New Zealand Forest Ranchers believe that "any organized, paid pig-destruction party equipped with good dogs and working areas systematically, would soon exterminate the pest."

Dogging is strictly a controlled management technique and for a specific function along a predetermined segment in a management unit. In view of the problems with hunt-dogs (see below), it will be desirable for the Park to establish a dog training unit, preferably in Kipahulu, for the sole purpose of breeding well trained pig dogs. Local expertise can be assembled from several Hana residents. The following recommendations are made: (1) a key person be appointed to head the dog training unit and to train two other handlers; (2) use only an all-male dog team; (3) only handlers be directly responsible for dogging; (4) teams of dogs for a control task to be leased when not on the job; (5) each dog team to comprise of two trackers (scent dogs), one mouth dog, two fighters and one catcher; and (6) whenever possible, dogging to be carried out downhill and along flush-lines no greater than 0.5km.

(iii) Hunting.—Sustained human hunting pressure is effective in reducing or manipulating pig populations in accessible reserves, agricultural lands and parks in parts of Europe, New Zealand, Australia and Malesia. In 3 of 13 National Parks with free-ranging pigs, populations were effectively reduced when hunting was permitted (Singer 1981).

The Valley below 700m has been hunted by Hana district residents for about 30 years. Hunting activity declined since 1969, when the Valley was deeded to NPS. Prior to this, about 200 pigs were harvested annually for table meat, in contrast to an annual estimate of 50 for the years 1978-1980. Access to the Valley became increasingly difficult in 1980, with all gates leading to the mouth of the Valley secured by the Hana Ranch Company. There was no hunting in the Valley during the first half of 1981.

Hana residents believe local hunters can effectively control pigs if there is greater access to the Valley. They value their usefulness to the Park management interests in the area. Hunting is, however, not recommended as a control tool especially in units 1, 4 and 5 for the following reasons:

1) Hunting will not eliminate pigs or reduce populations to a low minimum, as there is a minimum density beyond which rational hunters will not hunt. Hunting effort will decrease as the number of trips per hunter per pig or the expenditure per trip per hunter increases.
2) Hunters frequently borrow dogs or combine theirs with those of others. These dogs do not function as a team and "lost" dogs may turn feral.
3) Hunting has a dispersive effect and may change movement patterns in the uphill direction.
4) Hunters frequently hunt at their own convenience.
5) Hunters selectively kill adult animals and thus harvest from the top. Juveniles and animals below 30kg are not shot.
6) Hunting as a management tool is contrary to the legislative mandate of the Park and NPS.

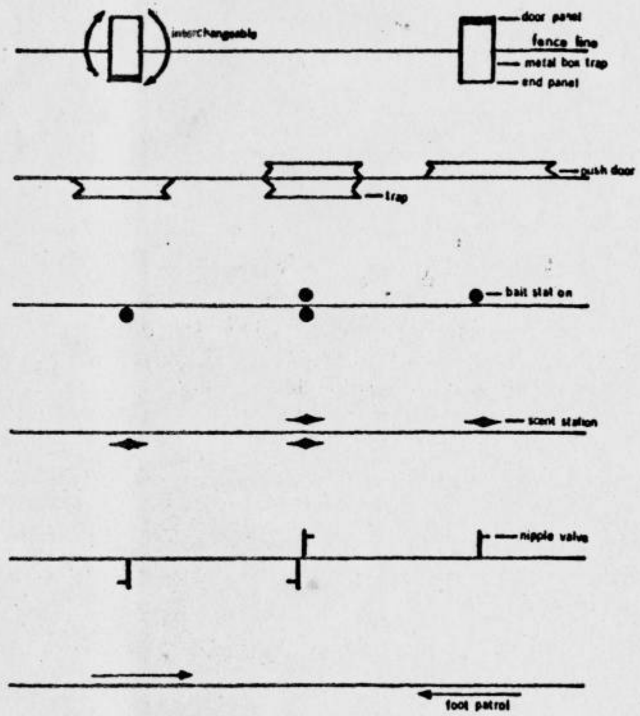
(iv) Fencing.—Kipahulu Valley has rugged terrain on which it would be difficult to erect, run and maintain fences. Notwithstanding, some fence lines will eventually be necessary to prevent pigs from moving into the Valley or to exclude them from management unit(s).

Possible variations on a fencing plan are: (1) fence the head and mouth of the Valley, (2) perimeter fencing of entire Valley, (3) fence individual plateaus, (4) incremental fencing of management unit(s), and (5) fence only entry-exit and interplateau movement routes.

It will be desirable to consider fencing only after other control operations (trapping, dogging and shooting) have been applied. Alternative (5) can be considered after initial reduction. It may be desirable to determine whether an exclusion fence line is necessary and erectable between units 1 and 5 to protect ohia forests from invasion by pigs from lower elevation forests. Another consideration is for a fence line between units 1A and 1B to contain self-maintaining strawberry guava below this elevation and to prevent pigs from dispersing the guava above this elevation. The management function of this and other fence lines is illustrated in Figure 39. Because unit 2 can be reached by pigs from unit 3, it will be desirable to consider exclusion fences for unit 2. All fencing operations should attempt to use the principle of discontinuous fencing by using suitable topographic features as fence line extensions.

Once fencing is adopted as a management tool, it will be necessary for the Park to consider: (1) effective ways of maintaining fence lines, (2) ways of maximizing the life of fence lines, (3) catastrophic events in the Hawaiian Islands and their possible effects on fences,

Figure 39: Examples of some management functions that could be built into fencelines separating two management units or along perimeter fences. Installations of the illustrated management activities and their actuation will enhance the usefullness and functions of fences in a feral pig control program.



Management activity	Management objective
- to include metal box trap as part of fence line - to interchange door and end panels when necessary	- to trap pigs from one or both management units
- to build in fence traps along fence line	- to trap pigs from one or both management units
- to set up bait stations - to experiment with food (solid) baits and chemically innoculated foods	- to attract pigs to traps or sites on fence line - to determine bait success and associated problems
- to set up chemical scent stations	- to attract pigs to scent stations - to determine feasibility of scent(s) for attracting attracting pigs to bait or poisoning sites
- to install auto-shut stainless steel nipple valves - to accustom pigs to obtain fluid (eg. molasses water) from valves	- to determine feasibility of introducing liquid toxicant into such installations during eradication phase
- to walk fence line	- to check integrity of fence line and perform maintenance work - to shoot pigs on sight

Figure 39: Examples of some management functions that could be built into fencelines separating two management units or along perimeter fences. Installations of the illustrated management activities and their actuation will enhance the usefullness and functions of fences in a feral pig control program.

(4) available fencing technology, relevant to rain forest habitats, and (5) possibility of installing simple telemetry devices for checking fence line integrity.

In view of tree fall or other threats to fences, the Park should experiment with parallel fencing in troublesome areas, e.g., at entry-exit routes.

Fences should possess other management functions and serve as more than just exclusion barriers. To achieve this, other control functions, either for immediate use to the unit or for experimentation for later use in other units, must be built into a fence line. Figure 39 demonstrates how control activites such as trapping, food and bait-lure experimentations, and poisoning could be built into a fence line. Boundary fence lines, e.g., between units 1 and 5 could have two different kinds of management activities on both sides.

(v) Poisoning.—Several poisons have been used effectively to control feral and wild pig populations in parts of New Zealand (MacKintosh 1944); Australia (Hone et al. 1980); British Borneo (Eaton 1925); Java, Indonesia (Hoogerwarf 1970) and Pakistan (National Research Council 1979). Tisdell (1982 - in press) provides a comprehensive treatment on the effectiveness, economics and philosophy of feral pig control using poisons. Between 70-80% reduction in a population can be achieved with the poison, sodium monofluroacetate (1080).

In the U.S., no toxicants have been registered for pig control, although clay pigeons, rotenone and zinc phosphide are being considered (Garner & Matschke 1981). Registration of a toxicant for pig control with the Federal Insecticide, Fungicide and Rodenticide Act necessitates 5-7 years research and an expenditure of 3-5 million dollars. While testing and development of pig toxicants are best handled by the Denver Wildlife Research Center, Colorado, the Park could provide feed forward information on habitat constraints to this agency. For instance, the established and suspected ecological relationship between feral pigs and birds, stream biota, mongoose and dogs should be known during the toxicant research and testing phase. In the interim, the Park should only consider use of the already proven and acceptable control tools.

Toxicants (solid or liquids) can perform what other control tools cannot, and thus have a place in feral pig control. Its option for control depends heavily on the list of absolute and essential criteria the Park sets for itself. Quantitative evaluation of other control operations should have been undertaken first before deciding on the <u>when</u> and the <u>technique</u> for using poison. Whenever possible, starchy and sugary baits are to be preferred over raw protein for bait inoculation. Liquid toxicants can be introduced from fixed drippers (Figure 39).

The following situations would be the most appropriate applications if poisons become a feasible means of control in the Valley: (1) at low pig density, i.e., below the regulated stabilized level; (2) when the Park determines that the threshold tolerance is not acceptable to ecosystem management; (3) as a follow-up or mopping up operation to further reduce or free an area of pigs; (4) when it has been established from a pilot study in a similar rain forest that the toxicant will satisfy absolute criteria such as to be non-environmentally polluting and non-lethal to non-target species; (5) when it is agreed upon to abandon the utilitarian aspect of the control program; (6) when remnant populations exhibit chronic avoidance behavior towards other management tools; (7) when reinvasion occurs in a unit; (8) when cost per unit effort in other management methods is too prohibitive; (9) when the Park decides to initiate the third term objective; and (10) when total pigs killed by all other control methods is less than the annual recruitment rate.

When a decision on poisoning as a control tool is reached, it is further recommended that the Park explore the possibility of making toxicants a "triple-ball cartridge" to control, in addition to the pig, the mongoose and rodents. Needless to say, a scientist experienced in environmental toxicology should be engaged in the preplanning and operational phase of this program. The Park should consider availing itself of the expertise of Animal Damage Specialist, C. P. Stone at Hawaii Volcanoes National Park.

Some Considerations on Control Operations

It is recommended that the Park use a matrix form of organization in planning its control operations (Table 47). This organization gives equal emphasis to management units as it does to term objectives.

Table 47: Example of a matrix form of organization for management units and programs in Kipahulu Valley.

Management units / Management programs	1		2	3	4	5
	A	B				
Reduction (short term objective)						
Stabilize population at regulated low level (intermediate term objective)						
Eradication (long term objective)						

A multi-approach program is recommended over one which uses one managment tool at a time. While the latter may facilitate monitoring of some habitat or operational variables, an integration of methods will contribute to more effective control. It is further recommended that management activities be conducted on a 4 month-2 month recess-4 month control cycle; this cycle to continue until the short term objective is reached. A management plan combining multi-approach methods and duration of control operations for the control units is illustrated in Table 48.

It should be stressed that once control is initiated, it will be desirable to run the control cycle until the population is stabilized to a low density. Haphazard control at discrete or irregular intervals will only increase population variance.

Because of geographic constraints, it is difficult for the present Park resource manager to effectively coordinate activities of feral pig control in the Valley. It will be desirable for the Park to create two to three resource management positions plus three seasonal resource management positions in Kipahulu district; this position preferably filled by Hana residents.

Interest in pig control activities has been indicated by Hana residents. A man-power pool can be formed by inviting interested individuals from Hana district. This pool can then be fragmented into three teams, each with three to five people. Two teams could operate on any one day, though not in the same unit.

Table 48: Management options for the reduction and eradication of feral pigs in Kipahulu Valley.

Management tools	Reduction (Short term objective)						Eradication (Long term objective)					
	Management units						Management units					
	1A	1B	2	3	4	5	1A	1B	2	3	4	5
Dogging and Shooting	●	●	●	●	●							
Livetrapping	●	●										
Deadtrapping					●	●	●	●	●	●	●	●
Hunting			●	●								
Poisoning							●	●	●	●	●	●
Fencing	●						●		●			●

The Park should explore effective ways of disposing of digestive tracts of pigs harvested from August to January. If necessary, these should be buried to a minimum depth of a foot in a marked site.

Consideration of the Interests of the People of Hana District

Feral pig control is an emotional subject in Hana. It is one issue which will unite the community into one resolve. The Park should not consider pig control without understanding the interests of Hana District residents. Some understanding on this issue is relevant to the Park's program.

There are two generations of hunters in Hana. Hunting is largely a family or group activity. Fathers have taught hunting skills to their children at a young age. Hunter and non-hunters alike are equally vocal on the usefulness of the feral pig to community members as a desirable food for local festivities, as well as a supplement to food budgets. Feral pigs were shot from the roads and near the coastline in the 1950's and 1960's, but land-use changes have pushed pigs into the upper pastures and forests. The pressure to obtain table meat from the forests has been reduced by the food stamp program. Regardless, the utilitarian value of the feral pig is never disputed in the community.

Resistance to pig control is primarily based on fears of insular approaches and poison. Poisoning, it has been expressed, will contaminate drinking water, kill coastal and stream fauna and endanger hunters and their dogs to poisoned pigs. For these reasons nearly the whole community is opposed to poisoning for controlling pigs.

The community has a different perception of the feral pig problem as outlined above. Some extreme reasons given by local residents for not favoring control are:

1) Pigs cause no damage to forests.
2) Hunting and human mobility in the forest are easier in areas with pigs than in those with fewer or no pigs.
3) Hawaiians lived with pigs; it's part of the heritage.
4) The need to enter the forests for medicinal or food plants no longer exists, so pig control is not necessary.
5) Pigs can control themselves, if not, hunters can reduce them.

The Park should acknowledge the people issue and treat it as a subsystem of the whole program. With an understanding of the <u>feral pig</u>, <u>habitat</u> and <u>people</u> problems, the Park manager could view pig control as a pig-habitat-people management triad. Specifically, the Park should emphasize that: (1) the evidence suggests that without pig control, forests as Hawaiians knew them will be overrun by exotics, and (2) Kipahulu Valley is an isolated ecosystem which NPS is to maintain in pre-Hawaiian or Hawaiian status. Public meetings between the Park and community should be encouraged so that both sides can better understand the feral pig issue and to examine responses to the question, why control feral pigs?, and to improve Agency-Community communication. Behind it all, the Park's objective should be to stimulate a commitment to it's cause, and to win public support for its goals and objectives.

Research Direction

Thirteen National Parks, inclusive of Haleakala, are presently plagued with feral and wild pig problems (Singer 1981). Decisive management decisions in most of these Parks cannot be made because of the lack of information on habitat impacts, population estimates and management strategies. Control methods are often not appropriate without modification to another area. The Park should, during feral pig control operations, undertake to conduct clearly defined research which has direct application to its overall management program. This research activity should not focus on the pig's basic biology, much of which is now known.

Quantitative methods can be used to collect impact data and monitor plant community dynamics. Useful information on habitat impacts and insights into the niche of the pig in the rain forest can be derived from stomach analyses. Ecological effects of control operations on species other than feral pigs should be studied. Suspected ecological relationships between the pig and native birds, stream biota and land snails, attended to in this study, merit further investigation.

Scientific documentation on habitat recovery must be undertaken once control activities for term objectives are initiated. This information has wide management implications and feedforward values. If incremental or exclusion fencing is adopted, fenced unit(s) regardless of pig density status should be monitored at regular intervals for habitat response to pig control.

Population statistics can be expected to change with control intensity or methods. Quantitative evaluation of control programs should be undertaken by collecting biostatistical (age, sex, fetal and litter counts, group size, numbers killed during dogging) and operational (man hours, distance covered, cost) data. Such an evaluation will yield information on relative cost-effectiveness for each control tool at varying pig density and changes in population structure with control programs.

Because pigs are macrosomatic animals, emphasis should be placed on research aimed at attracting (food bait, scent lures) or repelling pigs using their olfactory modes of orientation. Salivary and testicular pheromones (delta-16-androstene) in boars function to stimulate sows from a distance for courtship (Sink 1967; Melrose et al. 1971). Sexual pheromones have promise as an attractant and should be experimented with under field conditions. Synthetic androstenol pheromones have been used with success in several commercial pig farms in the United Kingdom. Live bait, using an estrus sow or one artificially induced, has limitations. It would be more desirable to experiment with scent lures for sows than boars. Novel baits such as alcohol and those that serve to simultaneously lure and hold pigs (Barrett 1979 - pers. comm.) should be studied.

This report concludes by recommending a pool of expertise to the Park, and comprising locally, C. P. Stone; nationally, R. H. Barrett and internationally, W. L. R. Oliver at the Pigs and Pecarries Specialist Group, Channel Islands, United Kingdom. These people can function to keep the Park updated on pig control technology, guide in the decision making process and serve as a general consultative body.

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.

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