ALIEN ANIMALS IN HAWAI'I'S NATIVE ECOSYSTEMS: TOWARD CONTROLLING THE ADVERSE EFFECTS OF INTRODUCED VERTEBRATES

Charles P. Stone

ABSTRACT

The adverse effects of introduced birds and mammals on native taxa and ecosystems in Hawai'i have been long term, widespread, and severe. Impacts began at least 1,500 years ago with colonization by the Polynesians and their flora and fauna, and continued with their increasingly severe disturbance to the landscape, especially below 500 m elevation. Problems accelerated with the arrival of continental man in 1778, and continue to the present day with suspected deliberate releases of birds that threaten native species as recently as 1982. Alien vertebrates can affect native biota through predation, competition, depredation, and habitat degradation. Negative impacts can be subtle or dramatic, but evidence of importance is manifested in large percentages of extinct and rare taxa. In this paper, adverse effects of major bird and mammal introductions are outlined where possible for islands, vegetation zones, and rare taxa. Although much remains to be learned, suggestions for reducing negative effects of alien vertebrates can be made. These include: Enforcement of efficient quarantine procedures; sufficient support for enduring and complete vertebrate damage control programs (including research, management, and monitoring) on lands managed for preservation of native Hawaiian ecosystems and taxa; development of multiple and adaptable methods of vertebrate damage reduction; preservation and management of the most intact areas remaining in Hawai'i; and cooperation and communication among the agencies and special interest groups (including developers and conservationists) in land use planning on regional bases. Cooperative approaches, effective education and communication about the value of protected areas, and the increased usefulness of such areas for all citizens, are seen as particularly important in reducing continued damage to Hawai'i's remaining native ecosystems by alien vertebrates.

INTRODUCTION

Adverse effects of introduced or alien vertebrates on native Hawaiian ecosystems and organisms may be divided into 2 categories: those that occurred largely in the past (including the introductions of the early Polynesians), and those that occur at present. The first are of interest because they provide examples of the devastating effects that aliens can cause over time to native species with small population sizes and inadequate defenses against intruders. Such early disruptions, when viewed in accurately constructed and comprehensive historical contexts, can provide insights into compositions and functions of the Hawaiian biota at a time when it was more intact. The effects of past introductions also provide sufficient warning to provoke caution about future introductions or translocations. The adverse impacts of some of these introductions are unknown, but the effects of others are clearly visible today.

Ongoing and active disturbances by alien vertebrates are of interest for 2 additional reasons. First, they allow direct observation and manipulation through which one can obtain understandings of the ecology of aliens and interrelationships within ecosystems. Secondly, through reduction, exclusion, or elimination of problem animals, entire ecosystems (or important components thereof) can be rehabilitated to some degree (see Lamoureux, this volume). Where ecosystem deterioration caused by introduced animals can be stopped or slowed, systems may at least function with primarily native components; and natural processes (including nutrient cycling, gene flow, succession, and evolution), although not pristine, may also be less influenced by man and his induced changes.

Damage caused by alien vertebrates to native flora and fauna in Hawai i may be categorized as predation, competition, depredation, or habitat degradation. Predation is the killing of one animal by another, and includes such important examples as the eating of eggs and young of birds by mammals, and consumption of insects and snails by mammals or birds. Competition is the negative influence of one animal on another when a resource needed by both is somehow limited. Relationships among native and exotic birds and a common food supply, and relationships among native birds, introduced rats and common food or nest sites, are examples. <u>Depredation</u> is the eating or otherwise destroying of plants by animals. Consumption, trampling, or uprooting of native plants (or plant parts) by alien mammals are examples. Depredations on plants influence other animals through impacts on their habitats, and these will be discussed under "Habitat Degradation."

Introduced vertebrates can have additional, subtle effects on native ecosystems and biota. Disease can be transmitted to native species through alien vertebrate reservoirs (see van Riper and van Riper, this volume). Introduced animals can disperse alien plants and thus increase plant densities, rates of spread, and distributional limits. Vertebrates sometimes also enhance germination of introduced plants through seed scarification in digestive tracts, or through digging up and/or fertilization with feces of potential seedbeds. Serious long-term damage can be caused by some alien vertebrates that disrupt nutrient cycling, initiate and accelerate erosion, radically change compositions of plant and animal communities, and alter evolution of other species through disruption of natural selection.

The purpose of this paper is to address some of the complexities of damage caused to native terrestrial ecosystems by birds and mammals introduced to Hawai'i by man. Introduced reptiles and amphibians also affect native species, particularly invertebrates (Howarth, this volume), but there is little information available about what are probably less severe impacts, at least currently. A brief summary of adverse effects prior to the arrival of European man will be presented, and the distribution of different kinds of impacts will be outlined by island and by general vegetation type. Management strategies for different animals and situations will be discussed and research needs identified. A coordinated approach to the management and research of introduced mammals and birds in Hawai'i's threatened ecosystems will be suggested.

POLYNESIAN IMPACTS (400 A.D. -- 1778 A.D.)

Beginning at least in 400 A.D., human colonizers of the Hawaiian Islands began arriving with their attendant land use practices, flora, and fauna. Vertebrate introductions included domestic pigs (Sus scrofa), red junglefowl (Gallus gallus), dogs (Canis familiaris), Polynesian or Pacific rats (Rattus exulans), and various stowaway reptiles (Kirch 1982). Although documentation is lacking, rats probably began to affect lowland invertebrates and plants shortly after human arrival; predation on low- or ground-nesting forest birds and seabirds would not be unexpected based on similar activity in historical time (Kepler 1967; Atkinson 1977; Imber 1978). Junglefowl, rats, and the other small vertebrates spread into lowland forests at rates dependent mostly upon genetic and behavioral adaptation to changing Hawaiian environments. High reproductive rates, low predation, and shortage of competition may have favored these small vertebrates in suitable habitat, especially that modified by man. However, on the whole, the continuing land modification facts of their introduced animals on the biota (Kirch 1982).

According to one estimate, about 80 percent of the lowland forest (below 500 m) was drastically altered by widespread use of fire, by agricultural and aquacultural development, and by forest clearing (Kirch 1982). Evidence of agriculture has been found as high as 1200 m in elevation (McEldowney 1983), and slash and burn agriculture was perhaps used to maintain pili grasslands (Kirch 1982) for thatching huts; <u>Sadleria</u> spp. and arrowroot (<u>Tacca leontopetaloides</u>) were used as pig fodder and famine food (McEldowney 1983). Descriptions of the early landscape were given by European explorers such as Cook and King, Vancouver and Menzies, and Chamisso (Olson and James 1982), and the impacts of Hawaiians on native vegetation are usually inferred from this.

A human population of perhaps 200,000-250,000 at the time of European contact (Schmitt 1971) may represent a decline resulting from reduced carrying capacity (Kirch 1982). The effects of such large numbers of people and their alterations of the native vegetation were undoubtedly large. Impacts on avian species alone were enormous, with 39 [now 45] of Hawai'i's 80 [now 86] known species of birds eliminated prior to the arrival of Western man in 1778 (Olson and James 1982). Most of the 13-15 flightless species of birds were probably hunted to varying degrees and eventually extirpated. Development of irrigated fields may have resulted in larger populations of the endemic Hawaiian duck (Anas wyvilliana), common moorhen (Gallinula chloropus), American coot (Fulica americana) and blacknecked stilt (Himantopus mexicanus) as residents. Establishment of the short-eared owl (Asio flammeus) may have been aided by man's introduction of the Polynesian rat (Olson and James 1982).

Dogs and pigs were valued by Hawaiians as scavengers and as sources of animal protein (Handy and Handy 1972; Kirch 1979), and were probably usually kept under control. Junglefowl and their eggs may have been less favored for food (Handy and Handy 1972) than some other sources, and may therefore have been less controlled; they formerly ranged from sea level to 2,100 m on Hawai'i (Schwartz and Schwartz 1949). Junglefowl also may have arrived later than other domestics (Tuggle 1979), but this is uncertain. Handy and Handy (1972) noted that pigs were allowed to "run about the kauhale (homestead) and gardens while they were young, but when they were sizable and ready for fattening they were penned inside enclosures of heaped-up stones." Whether this was always the case is unknown. Recent evidence

suggests that pigs sometimes were separated from gardens and irrigated fields by keeping them within village walls (D.B. Barrere, pers. comm.). Pigs probably existed throughout most of the islands by the time of European contact (McEldowney 1979), and feral populations in "moist" forests could have been "an older utilized resource" (McEldowney 1983). Whether they were important invaders of Hawaiian rain forests is unknown. As on other Pacific islands such as New Guinea, some pigs may have been tightly managed and herded with dogs; some may have been caught at times from nearby forests and fallow fields; and some may have been semi-wild or pariah (Diong 1983) populations, fed and even called in by people as needed (H. McEldowney, pers. comm.).

The reportedly small size of Polynesian pigs may have been less a function of genetics than a diet low in protein and the rapid use of younger pigs for food. P.V. Kirch (pers. comm.) noted that most pigs recovered from archaeological sites are young and that pigs were fed coconut, sweet potato, and breadfruit. Pigs also ate human wastes and thus served as a means of village sanitation. Handy and Handy (1972) suggested that feral pigs in upland areas subsisted on fruits, nuts, seeds, and various ferns, and that they "grubbed for roots." Considerable acreages of fallow land and secondary growth (McEldowney 1983) may have served to attract foraging feral pigs more than dense rain forest.

Animal protein is required for maximum growth and reproduction of pigs (Pond and Houpt 1978; National Research Council 1979), and other than turtle eggs, fish, and beached marine mammals from a sometimes capricious ocean, there were few protein sources in native, as opposed to man-influenced, ecosystems. (Animal protein may have declined as human populations increased, as it has elsewhere, e.g. Kirch and Yen 1982.) Thus, feral pig populations that existed in rain forests prior to Cook's arrival may have been comprised of small-sized pigs at low densities. What is known about nutrition, pig husbandry practices, and agricultural land use would seem to suggest that modifications of the interior rain forest vegetation by Polynesian pigs was not great.

EFFECTS ON ISLANDS AND ECOSYSTEMS

Although Polynesian introductions and land use resulted in changes that continue to the present day, subsequent deliberate and accidental introductions and practices of early explorers, settlers, agriculturists, hunting groups, bird clubs, and governments caused additional modifications. More comprehensive histories of vertebrate introductions and distributions are given

elsewhere (Tomich 1969; Kramer 1971; van Riper and van Riper 1982; Berger 1974, 1975, 1981), and will not be repeated here.

The effects of the alien vertebrates now present are complex, varied, and subtle. Some of the direct effects on different vegetational types and the biota of the Hawaiian Islands will be mentioned in this section. As indicated earlier, the general headings will be depredation, predation, competition, and habitat degradation. A complete treatment is not possible, but what is considered most important will be stressed. Illustrations of indirect effects and of the complexities involved in reducing alien influences will then be presented. More succinct statements about problems and ongoing and proposed solutions will be found in a subsequent section. A diagram of general impact of important vertebrate taxa is presented in fig. 1 (after Scott et al., in press). A much condensed table of rare plant taxa threatened by alien vertebrates (table 1) was adapted from the more complete treatment by Wagner, Herbst, and Yee (this volume).

Depredation

Domestic and feral cattle (Bos taurus). Cattle were "historically abundant on Kauai, Oahu, Molokai, Maui, and Hawaii" and heavily overstocked on Lana'i (Tomich 1969). Feral cattle were eliminated by the mid 1900's on O'ahu, and probably Moloka'i more recently, but still exist on Maui (L.L. Loope, pers. comm.) and Hawai'i. Present distribution on Hawai'i includes the South Kona District, Mauna Loa, and Hamakua and Puna forests. Cattle are present in remote forests, in subalpine scrub, or on inaccessible lava flows on ranchlands (Tomich 1969; R.L. Walker, pers. comm.).

These animals have serious negative impacts on the vegetation of dry, mesic, and wet forests at low and high elevations. According to Scott et al. (in press):

Domestic and feral cattle have been overall the single most destructive agent to Hawaiian ecosystems, particularly to mesic forests... Koa reproduction is completely suppressed by grazing (Baldwin and Fagerlund 1943), and cattle are mostly responsible for converting large tracts of forest to open pasture on south and northwest Haleakala, lower elevations of west Maui and Lanai, much of Molokai, the dry side of Kohala Mountain..., the Waimea plains, the north side of Mauna Loa below 2200 m elevation, the mesic and west slopes of Hualalai, most of south

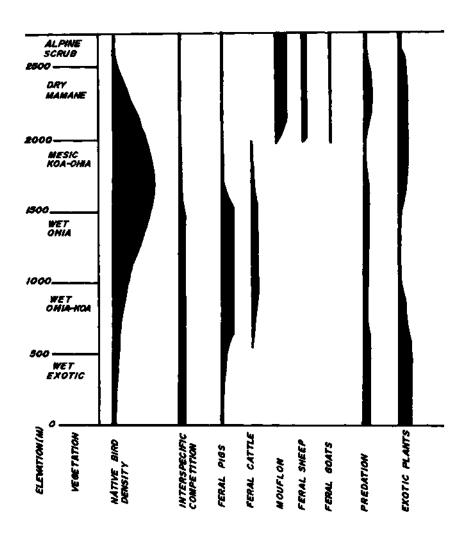


Figure 1. Stresses on native bird populations in Hawai'i (adapted from Scott et al., in press).

Table 1. Native Hawaiian plants listed as endangered (L), proposed for listing (P), or candidates for review by the U.S. Fish and Wildlife Service (C), that are also thought to be harmed by alien vertebrates.

Taxon	Distribution ²	Status	Threats ³
Haplostachys haplostachya var. angustifolia	H	L	Feral goats, sheep, fire, alien plants, military
Vicia menziesii	н	L	Cattle, logging, pigs, reforestation, rodents
Gouania hillebrandi	М	L	Feral and domestic livestock, alien plants, insects

L

С

С

С

Livestock, fountain grass,

Axis deer, cattle, goats,

Feral animals, especially

mouflon; removal of fruit

Feral cattle, goats, pigs, alien plants, fire, military

rodents, fire

insects, fire

for propagation

Н

H,L

Н

0

Kokia drynarioides

Abutilon menziesii

var. sandwicense

Cyanea superba

Argyroxiphium sandwicense

Gardenia brighamii	O,Mo,L,M,H	С	<pre>Introduced herbivores, fire, agriculture, alien plants, rodents,insects</pre>
<u> Ribiscadelphus</u> <u>distans</u>	ĸ	С	Feral goats, vandalism, fire, rats, insects
Mezoneuron kavaiense	к,о,м,н	С	Domestic and feral animals, alien plants, rodents, fire,

Status

С

Distribution²

М

 $\mathtt{Threats}^3$

wood harvest, insects

Feral and domestic animals

Domestic and feral animals,

agriculture, alien plants, rats

Santalum freycinetianum var. <u>lanaiense</u>	L,M	С

Taxon

Remya mauiensis

¹ Adapted from Wagner, Herbst, and Yee (this volume).
2 Hawai'i, Lana'i, O'ahu, Moloka'i, Maui, Kaua'i.
3 Botanists can also threaten some species.

Kona, and the slopes between Mauna Kea

and Kilauea. A consistent pattern of cattle invading wet forests from adjacent mesic areas occurs at ecotones on Maui and Hawaii, and formerly occurred on Kauai before control in the 1920's to 1930's...

Cattle were involved (with goats and sheep) in removing much of the native dryland forest on Ni'ihau and Kaho'olawe (Wagner, Herbst, and Yee, this volume). They have severely reduced mamane (Sophora chrysophylla) trees on Parker Ranch on Hawai'i (Scowcroft 1983). McEldowney (1983) summarized some of the drastic impacts on vegetation, soil and water supplies in the Waimea area in the mid to late 1800's but suggested that the native forests were reduced by Hawaiian land use practices as well as cattle depredations.

In addition to causing forest destruction and fragmentation, cattle have seriously threatened and probably caused the extinction of many native plant taxa. Cattle currently threaten rare plants such as <u>Vicia menziesii</u>, <u>Abutilon menziesii</u>, and <u>Cyanea superba</u> (table 1). Cattle reduce native plant diversity and simplify structure, composition, and function of vegetation near the ground. The effects of severe grazing pressure on plant gene pools, nutrient cycling, and, plant evolution (through natural selection) are undoubtedly severe.

Feral sheep (Ovis aries). This species occurs from 600-3,600 m on Hawai'i. It is present chiefly on Mauna Kea and Hualalai, although it descends to sea level in the Ka'u District (Tomich 1969; van Riper and van Riper 1982). Feral sheep have not been seen on Kaho'olawe since the early 1980's (R.L. Walker, pers. comm.).

Sheep mainly damage dry areas above 1,000 m on Hawai'i. Their effects on mamane reproduction can be extreme, especially near tree line (van Riper 1980; Scowcroft 1983; Scowcroft and Giffin 1983). Feral sheep compact soil and increase erosion through establishment and repeated use of trails. Sheep were implicated with goats and cattle in the destruction of much of the native vegetation of Ni'ihau and Kaho'olawe (Wagner, Herbst, and Yee, this volume). Feral sheep are a threat to the Federally endangered Haplostachys haplostachya var. angustifolia, (table 1), Mauna Kea silversword (Argyroxiphium sandwicense var. sandwicense), Stenogyne diffusa, S. microphylla, and probably other rare taxa in Hawai'i's dry uplands.

Mouflon (Ovis musimon). Mouflon are established on upper Mauna Loa and Mauna Kea on Hawai'i, and in the dry kiawe (Prosopis chilensis) forests of Lana'i (Tomich 1969; van Riper and van Riper 1982). In the mamane forests of Mauna Kea, they have effects on the vegetation similar to those of feral sheep (Giffin 1982). In subalpine 'ohi'a (Metrosideros polymorpha) and alpine scrub in the Ka'u District on Hawai'i, they also damage Ka'u silversword (Argyroxiphium kauense) and other native plants; on Mauna Kea, they threaten A. sandwicense var. sandwicense. On Lana'i, mouflon apparently do not penetrate native forest (Scott et al., in press).

Feral goats (Capra hircus). Goats in Hawai'i now occur on all main islands except Ni'ihau and Lana'i, where they have been probably eliminated. They damage drier open ecosystems from low to high elevations. On Maui and Hawai'i, they are found in subalpine woodland and alpine grassland. Goats commonly enter upper elevation wet forest on Maui and in the past also destroyed wet forest remnants on Lana'i. On Moloka'i, Hawai'i, and Maui, goats degrade low elevation dry forest. On Kaua'i, they damage the edge of the Alaka'i Swamp and enter wet habitats in dry periods. Goats have had a major role in the destruction of dryland and mesophytic forest on Ni'ihau and Kaho'olawe in the past (Tomich 1969; Scott et al., in press).

Feral goats are implicated as threats to Haplostachys haplostachya, Abutilon menziesii, Cyanea superba, Hibiscadelphus distans (table 1), and other rare plants (Wagner, Herbst, and Yee, this volume). Effects on koa (Acacia koa) (Spatz and Mueller-Dombois 1973), silver-swords, Haleakala sandalwood (<u>Santalum hale</u>akalae), and other rare trees have been reported (Loope 1982, 1983a; Loope and Scowcroft, this volume). Feral goats had probably eliminated all traces of <u>Canavalia</u> kauensis except the seedbank in the lowlands of Hawai'i Volcanoes National Park. When goats were removed, dormant seeds sprouted, and the plant reappeared (Mueller-Dombois 1981). Goats limit mamane reproduction in Haleakala National Park, and apparently negatively affect reproduction of woody native species such as Canthium odoratum, <u>Dodonaea viscosa</u>, and <u>Osteomeles</u> anthyllidiofolia in Hawai'i Volcanoes National Park (Williams 1980).

Black-tailed and axis deer (Odocoileus hemionus and Axis axis). Blacktails are found on western Kaua'i in dry native and alien forests (Tomich 1969). [Koa and 'ohi'a are native elements of these forests; kukui (Aleurites moluccana) is a Polynesian introduction; and silk oak (Grevillea robusta) and several species of eucalyptus are aliens (Kramer 1971).] Axis deer are

found in lowland kiawe, strawberry guava (Psidium CATTLEIANUM), And Roa haole (Leucaena <u>leucocephala</u> forests and range into higher 'ohi'a forests on Molo-ka'i, Lana'i, and Maui (van Riper and van Riper 1982), with a small remnant on O'ahu. Blacktails have threatened rain forest and rare bird habitat in the Alaka'i Swamp in the past. Axis deer and pigs have badly degraded vegetation and soils of East Moloka'i, with attendant damage to coral reefs on the southern coast through siltation (Scott et al., in press). Axis deer are viewed as the most serious existing threat to Lana'i's remaining forest and are a potential threat to mesic and rain forest on Haleakala (Scott et al., in press). Invasion of adjacent rain forest by axis deer may follow creation of open forest by cattle, pigs, or goats.

Feral pigs (Sus scrofa). Feral pigs occur on all major islands except Lana'i and Kaho'olawe (Tomich 1969; van Riper and van Riper 1982). Pigs were apparently present on Laysan Island and Sand Island at Midway Atoll in the late 1800's and early 1900's (Kramer 1971). On Kaua'i, O'ahu and Maui, pigs are restricted to rain forest and grasslands on ranches (Giffin 1978) or in the subalpine forests of Haleakala National Park (Jacobi 1976). According to Giffin (1978) and Kramer (1971), pigs are abundant on Ni'ihau in arid and open areas with kiawe (Zone A of Ripperton and Hosaka On Hawai'i, pigs are found from coastal dry-1942). lands through rain forest to the upper slopes of Mauna Loa and Mauna Kea. They have been observed at 3,030 m. according to van Riper and van Riper (1982). In mamane woodlands of Mauna Kea, densities are much lower than in rain forest (Giffin 1978), where pigs apparently reach levels (19-79 /km²) unmatched elsewhere (Singer 1981).

Feral pigs are the major current modifiers of Hawaiian forests, probably even exceeding damage done by man. Pig damage has reached extreme levels in this century, perhaps as a result of increasing densities as well as expanding distributions. The reasons for this are unclear, although it has been postulated that animal protein in the form of earthworms, and mutualistic relationships with certain dominant alien plants (e.g. Passiflora mollissima, Myrica Psidium cattleianum, fava), have made conditions more favorable for pigs than previously (Diong 1983). Man and pigs together seem to be enhancing pig habitat over time, favoring introduction of alien plants and resulting in accelerating damage in many areas. The role of wild dog control (through poisoning and other means) in recent creation of more favorable pig habitat in some mesic and dry forests is unstudied.

Pigs compound and intensify the problem of alien plant ingress by creating open habitats through digging up, eating, and trampling native species, and by increasing soil fertility. Pig activity thus works against reestablishment of many native plants adapted to poor soils, and favors establishment of alien plants (this will be discussed further in the section entitled "Nutrient Cycling"). Pigs also transport plant propagules in their feces and pelage. The spread of alien weeds since 1945 in Kipahulu Valley seems well correlated with pig range extension (C.W. Smith and L.L. Loope, pers. comm.). Large areas can be affected by pig activity. It has been calculated that feral pigs in the Kilauea Forest Reserve on Hawai'i dig up over half of the diggable area in a year's time (Cooray and Mueller-Dombois 1981).

Alien plants enhanced by pig activity in Hawai'i, in addition to those noted above, include: Ageratina riparia, Rubus penetrans, Hedychium spp., Sonchus spp., Buddleja asiatica, Phaius tankervilliae, Anemone hupehensis, Andropogon spp., Paspalum spp., Setaria palmifolia, Solanum pseudo-capsicum, Psidium guajava, and Passiflora ligularis (J.K. Baker, unpubl. data).

That the exclusion or removal of pigs can result in recovery of native vegetation and changed plant composition has been quantified through exclosure studies in rain forests (Katahira 1980; Higashino and Stone 1982), and in subalpine grasslands (Spatz and Mueller-Dombois 1975; Jacobi 1976). Some native species seem able to remain stable or increase in the absence of pigs over varying periods of time in different areas, but continued disturbance often favors aliens. In subalpine grasslands in Hawai'i Volcanoes and Haleakala National Parks where pig disturbance continued, native Deschampsia australis and Panicum tenuifolium were replaced by Holcus lanataus (Spatz and Mueller-Dombois 1975; Jacobi 1976). Pigs severely damage fragile and limited communities, such as Haleakala greensword (Argyroxiphium virescens) and Oreobolus furcatus and Carex svenonis bogs on Hawai'i, Maui, and Kaua'i (Gagne 1982; Loope 1983a).

Feral pigs selectively take certain native plant species, thereby reducing already limited populations or confining them to high epiphytic strata (e.g. Astelia). Tree ferns (Cibotium spp.) and Sadleria spp. are preferred items, as are other ferns (e.g. Marattia and Pteridium), Astelia spp., Freycinetia, and various Lobeliaceae and Labiatae. Pigs trample Peperomia and break weak stems of native Cyrtandra, mints (Phyllostegia spp. and Stenogyne spp.), and orchids (Loope 1983b) and are specifically identified as a threat to the candidate endangered species Cyanea superba and the

listed <u>yiçin menziesii</u> (table 1)ı becdlings of domi-

Mant plants such as koa, mamane, and pilo (Coprosma spp.) may sometimes be taken in numbers great enough to affect forest composition, growth forms, and succession over large areas (Diong 1983; J.K. Baker, unpubl. data).

Black and Polynesian rats (Rattus rattus and R. exulans). Black (roof or ship) and Polynesian rats are found on all major Hawaiian islands (Tomich 1969; van Riper and van Riper 1982), often in the same vegetation type. Tomich (1969) indicated that black rats are also present on Sand and Eastern Islands at Midway and possibly other islands, whereas Polynesian rats may also inhabit Ni'ihau, Ka'ula (off Ni'ihau), Kure Atoll (at northeastern end of the chain) and some other islands. Although R. exulans characteristically favors lowlands and R. rattus low and mid elevations (Tomich 1969; van Riper and van Riper 1982), both species are adaptable and found at higher elevations, sometimes in substantial numbers. The black rat occurs to 2,970 m around buildings at Haleakala National Park (Tomich 1969) and to at least 2,440 m in Hawai'i Volcanoes National Park The Polynesian rat has been trapped at (Tomich 1981). 2,060 m in Kipahulu Valley on Maui, and both species are common in wet koa and wet 'ohi'a and are present in scrub 'ohi'a vegetation types there (Stone et al. In Hawai'i Volcanoes National Park, black rats were 3 times as trappable in rain forest as in mesic forest (C.A. Russell and C.P. Stone, unpubl. data).

Black rats damage flowers, fruit, and bark of Hibiscadelphus (Baker and Allen 1976; Russell 1980), and bark of Osmanthus sandwicensis, Acacia koa, Coprosma rhynchocarpa, and Pittosporum spp. Damage to fruit of Pittosporum hosmeri and Santalum paniculatum has also been noted. The importance of rats as depredators and pollinators of Freycinetia (Perkins 1903) has recently been questioned (Cox 1983), but probably prematurely.

Black rats in rain forests at Hawai'i Volcanoes National Park consume green plants and seeds more frequently than adult or immature insects. Plants taken include Fragaria vesca, Rubus rosaefolius, Physalis peruviana, Vaccinium calycinum, and V. reticulatum. Seeds of Carex wahuensis, Microlaena stipoides, Paspalum dilatatum, and Sacciolepis indica were eaten (C.A. Russell and C.P. Stone, unpubl. data).

Black rats in mesic forests at Hawai'i Volcanoes National Park ate green plant material more frequently than insect larvae. Adult insects were taken even less frequently. Seeds dominated in summer diets and green plants in winter (C.A. Russell and C.P. Stone, unpubl.

data). Rat food habits and densities in different vegetation types are being further analyzed for populations in native forests of Kipahulu Valley and Hawai'i Volcanoes National Park.

House Mice (Mus musculus). This species has one of the most widespread geographical and ecological distributions of any of the alien mammals in Hawai'i. is abundant over a wide range of vegetation types on all of the main islands, at Midway Islands, and on many Mice range from sea level to 3,920 m (Tomich islets. 1969; van Riper and van Riper 1982). Data on comparative densities in vegetational zones are not available, but mice are probably most abundant in lowland habitats, and populations are known to sometimes erupt in "drier beach, grassland, scrub, and forest areas," for example on Maui, Hawai'i, and Kaho'olawe (Tomich 1969; R.L. Walker, pers. comm.). On Maui, substantial populations may exist in wet forests over 1,200 m in some areas, but not in others; possible reasons for this are under investigation (Stone et al. 1984). Little information on Mus food habits in Hawai'i is available, but in the lowlands, invertebrates, grass seeds, fruit, and other items are taken (Kami 1966). Much more needs to be known about the impacts of this ubiquitous alien on native Hawaiian systems.

Predation

Small Indian mongooses (Herpestes auropunctatus). Mongooses are present on all main islands except Kaua'i (possibly), Lana'i, Kaho'olawe, and Ni'ihau (Tomich The species ranges from sea level to above timberline and is generally most abundant at lower elevations (less than 600 m) on windward coasts. Small to moderate populations occur from 600-1,200 m in mesic vegetation (Baldwin, Schwartz, and Schwartz 1952) and in subalpine vegetation (Banko and Manuwal 1982; C.P. Stone, unpubl. data). However, at favorable locations, a strict elevational gradient may not hold. Limited data from Hawai'i Volcanoes National Park suggest twice as many mongooses in mesic forests at about 1,880 m as in rain forest at 1,160 m and one to several times as many animals at 30 m in coastal grasslands with alien grasses and shrubs as at higher elevations (C.P. Stone, unpubl. data; C.A. Russell and C.P. Stone, unpubl. data).

Mongooses undoubtedly disperse strawberry guava and other alien plants (Baldwin, Schwartz, and Schwartz 1952) and prey upon colonial seabirds (King and Gould 1967; Simons 1983) and marine organisms (LaRivers 1948; Baldwin, Schwartz, and Schwartz 1952), but for purposes of this discussion, predation on native land animals will be emphasized.

Predation upon Hawaiian crow or 'alala (Corvus hawailensis) fledglings (Giffin 1983) and nene (Neso-chen sandvicensis) eggs and incubating females (Banko 1982) are the most important obvious effects of mongooses on native animals in Hawai'i at present. Predation on nene in subalpine nesting areas where mongooses are often scarce may be less frequent than predation in the lowlands where mongooses are more abundant, but it is still a major mortality factor for geese. However, vegetational cover is also important: mongoose predation on pheasant nests was higher in areas of sparse vegetation at low altitudes than in areas of denser cover at higher altitudes, even though mongoose populations were apparently lower in the lower elevation/ sparse vegetation area (Smith and Woodworth 1951). Re-establishment of lowland breeding nene populations probably depends on mongoose reduction there, although other limiting factors such as nutrition may also be important (Banko 1982; Stone et al. 1983). Mongoose control in relatively undisturbed mesic koa-'ohi'a forest currently used by the 'alala (Burr et al. 1982) seems necessary. The rarity of red junglefowl on many islands has been attributed to cat and mongoose predation to a varying degree (Berger 1981). Effects of mongooses on low nesting forest passerines are unknown.

Baldwin, Schwartz, and Schwartz (1952) considered invertebrates, including Lepidoptera, Orthoptera, Coleoptera, Hymenoptera, Diptera, Isopoda, and Arachnida, to be important in the mongoose diet. That many of the taxa taken are alien, may be more a function of location of collections than an indication of little impact on native invertebrates. More information on effects of this opportunistic carnivore on birds, plants, and invertebrates in Hawai'i's native ecosystems is needed.

Feral cats (Felis catus). Feral cats occur on all main islands and on other islands in the chain. They were common in the forests of some islands by the mid 1800's (Scott et al., in press). Cats are probably most abundant at low and middle elevations, near human habitations, and in drier areas (Tomich 1969; van Riper and van Riper 1982), but they are found wild in remote areas such as Kipahulu Valley rain forests and in mesic forests at high elevations on Mauna Loa (C.P. Stone, unpubl. data).

Cats may have contributed to the extinction of the Hawaiian rail (<u>Porzana sandwichensis</u>) and are presently important predators on sea bird nesting colonies (Berger 1981; Simons 1983; J.L. Sincock, pers. comm.). Adverse effects on native terrestrial birds probably are limited to those that nest on the ground or low in the understory. Red junglefowl may have been extirpated by cats and mongooses on some islands, although other

factors were undoubtedly involved (Berger 1981). Effects on mene populations are unknown, but the nocturnal habits of cats might facilitate killing of females on nests as well as goslings. Forest birds that would likely be vulnerable because they forage in the understory include 'elepaio (Chasiempis sandwichensis), Hawaiian thrush or 'oma'o (Phaeornis obscurus), puaiohi (P. palmeri), Maui parrotbill (Pseudonestor xanthophrys), and po'ouli (Melamprosops phaeosoma), according to Scott et al. (in press). Young 'alala, as mentioned earlier, are also vulnerable when on or near the ground. Tomich (1969) reported lepidopteran remains in the tracts of 2 cats collected on Mauna Kea, but it is unlikely that the impact on native invertebrates is great. C. van Riper III (unpubl. data) found birds in 6 of 9 cat stomachs from Mauna Kea (5 with passerines) and rodents and snails in the other 3 stomachs. Cat stomachs and scats collected in native forests should be saved and analyzed so that a data base can be accumulated.

Black and Polynesian rats. The distributions of black and Polynesian rats are given above. Black rats were thought to have caused the extinction of transplanted Laysan rails (Porzanula palmeri) and Laysan finches (Telespyza cantans) at Midway Islands (Tomich 1969); to have been partly responsible for extinction of the Hawaiian rail (Berger 1981); and to adversely affect dark-rumped petrel (Pterodroma phaeopygia) colonies in Haleakala National Park (Simons 1983). Polynesian rats prey on Laysan albatrosses (Diomedea immutabilis) and other seabirds (Kepler 1967; Tomich 1969).

Past impacts of arboreal black rats on native forest birds are assumed to have been enormous (Atkinson 1977). Reductions of forest birds elsewhere in the Pacific followed introduction of black rats, and decreases of such forest birds as Maui parrotbill, 'o'u (Psittirostra psittacea), crested honeycreeper (Palmeria dolei), and 'akiapola'au (Hemignathus munroi) as a result of black rat irruptions in Hawai'i were suggested by Atkinson (1977). Rat predation (probably Ratus) may have helped reduce populations of the cavity-nesting Kaua'i 'o'o (Moho braccatus), according to Scott et al. (in press). Probably other cavity-nesting species have also been affected. 'Apapane (Himatione sanguinea) feathers were found in one of 86 stomachs from black rats taken in native rain forest on Hawai'i (C.A. Russell and C.P. Stone, unpubl. data).

Black rats were reported to prey on land mollusks by Perkins (1903). In the montane rain forest on Hawai'i, adult insects occurred in 32%, insect larvae in 17%, and annelids in 9% of 86 stomachs collected (C.A. RUSSell and C.P. Stone, unpubl. data). Adult and larval insects occurred more frequently in winter, and annelids in summer. Adult insects taken were in the orders Diptera, Hemiptera, and Hymenoptera, while larvae were in the orders Coleoptera and Lepidoptera. Further work on diets of both species of rats in Kipahulu Valley is under way under National Park Service contract with B.P. Bishop Museum (Stone et al. 1984).

Interspecific Competition

Native and alien birds. Banko and Banko (1976) concluded that 3 introduced avian species -- the common myna (Acridotheres tristis), Japanese white-eye (Zosterops japonica), and red-billed leiothrix (Leiothrix lutea) -- had potential roles in reducing populations of native forest birds, on the basis of habitat overlap and food habits. They traced the introductions and histories of populations of each species in Hawai'i. The barn owl, Tyto alba, was not believed to be a serious threat to the 'io, Buteo solitaris, or the short-eared owl, <u>Asio flammeus</u>, in the past or at present (Banko and Banko, n.d.). Competition for, and reduction of, such important lepidopteran taxa as Geometridae, Pyralidae and other food resources, especially during the nesting season of native birds, is presumed. Banko (1978) and Gagne (1980) also outlined the deleterious effects of continental flies and wasps on insects that were formerly important foods for 'o'u, Hawai'i creeper (Oreomystis mana), palila (Loxioides bailleui), and 'oma'o, among other species. Competition could have been particularly important at the height of alien bird population expansion (Banko and Banko, n.d.), especially if coupled with a diminished prey base resulting from insect predation, parasitism and diseases. Atkinson (1977), using a similar historical/ecological approach, also concluded that the melodious laughing-thrush or hwa-mei, Garrulax canorus, might be a factor in competition with native birds, based on widespread distribution of this species in Hawaiian forests. However, he judged that the introduction was too late to implicate the hwa-mei in major declines of native birds.

Ralph (1978) suggested that among 10 common passerines in Hawai'i Island forests, "interspecific actions appear to play a secondary role at most times." His data have not yet been fully analyzed or published.

Conant (1981) studied distributions and densities of 8 alien and 9 native birds on Mauna Loa and concluded that <u>Leiothrix</u> may have displaced the 'oma'o or Hawaiian thrush in mountain parkland, savanna and 'ohi'a dry forest. Although Japanese white-eyes invaded closed rain forest in considerable numbers, competition was thought to be of little importance in

controlling distribution of natives. Conant noted, however, that species densities could be limited to the detriment of less aggressive competitors around scarce nectar sources.

Van Riper (1976) hypothesized competition between the common 'amakihi, <u>Hemignathus virens</u>, and Japanese white-eye in 'amakihi territories. He found that although lack of mamane nectar could prevent breeding, excess nectar (provided by him) resulted in increased territorial defense and low breeding success (van Riper 1984). The precise influence of <u>Zosterops</u> was not determined in his study, but it could be crucial depending on food resources and population levels. Conant (1976) provided some evidence that common 'amakihi and 'apapane affect each other's densities depending upon whether or not nectar is the main food resource (if it is, 'apapane densities exceed those of 'amakihi); however, she noted that rainfall and other parameters [perhaps often including competition with <u>Zosterops</u>] may also define optimum habitats for both species.

Pimm and Pimm (1982) suggested that more dominant native species such as the 'i'wi, <u>Vestiaria coccinea</u>, and several extinct and endangered honeycreepers were less able to subsist on marginal resources than less aggressive competitors such as 'apapane and 'amakihi. Alien species such as <u>Zosterops</u> might adversely affect such dominants by forcing increased territorial defense at good nectar sites (preferred species with many blooms); by relegation to less favorable sites (preferred species with fewer blooms or secondary tree species); or through reducing and further dispersing an already dispersed nectar supply.

Scott et al. (in press) discussed distributions, habitat occurrences, and densities of alien bird species in Hawai'i. Space is not available here to cover possible competitive interactions species by species, but alien bird richness was highest in dry woodlands below 1,500 m with introduced plant understories. It was noted that few introduced gamebirds penetrate closed forests, and that disturbed habitats contain more alien bird species than undisturbed. Disturbed forests allow avenues of ingress for alien birds, according to the authors.

Mountainspring and Scott (in press) used partial correlation matrices for paired species (with habitat effects removed), to infer competition (for food) among alien and native forest passerines. The bulk of significant correlations were positive (67% of total), suggesting species association rather than competitive avoidance. The authors noted that such species as the omnivorous Zosterops, Leiothrix, and Garrulax; the

insectivorous 'clepaio, Kawa'i creeper (Oreomystis bairdi), 'akepa (Loxops coccineus), and common 'amakini; and the nectarivorous 'apapane and 'i'lwi showed positive associations. Increasingly or decreasingly favorable habitat for a particular guild was evidently similarly responded to by all species in the guild across a variety of locations on each island. The only consistent negative partial correlations (presumed to indicate competitive avoidance) were for Zosterops/Chasiempsis on windward Hawai'i and Zosterops/Vestiaria in montane forests on Hawai'i. Scott et al. (in press) hypothesized competition for understory insects to explain the first relationship and competition for lower quality (dispersed?) nectar to explain the second. As noted earlier, increased territorial defense by Vestiaria may be another (not exclusive) explanation for negative associations over the long term.

Native birds and rats. Atkinson (1977) noted that many Hawaiian forest birds depend on nectar or insects for food, but thought that many insects are unavailable to rats because they are too small or impossible for rats to reach. This generalization has not been investigated. Perkins (1903) pointed to the depredation of rats (probably the more arboreal R. rattus) on Freycinetia arborea fruit. Since 'o'u and 'alala also depended heavily on this fruit, rats may have especially competed with them when and where rats and 'o'u and/or 'alala were abundant (Banko and Banko, n.d.).

Based on our knowledge of rat food habits in Hawai'i (see previous discussions) it seems that direct competition would be likely for native birds that specialize on fruit and large conspicuous invertebrates that are active day and night. However, insect eggs, pupae, and many small invertebrates on and above ground level might be vulnerable to both birds and rats. Thrushes and perhaps po'ouli (a specialist on snails, according to Baldwin and Casey 1983) are among native birds that may compete with rats, in addition to species already mentioned. However, almost nothing is known of dynamic interrelationships among rats (both species), plants and invertebrates in thrush and po'ouli habitats. (The same interrelationships should also be studied in similar areas not frequented by those avian species, for comparison.) Information on rats and their adverse effects in other important forest bird habitat is also lacking, but preliminary data on rat densities and food habits and bird abundance from several areas in Kipahulu Valley are being analyzed (Stone et al. 1984).

Habitat Degradation

Optimum habitat for a native animal may be considered as the natural complex of physical and

biological factors in which a population is at a peak that can be sustained over time without damage to the habitat (carrying capacity). Introduction of most alien elements usually degrades the optimum habitat for native species. Alien diseases, predators, and competitors of vertebrates have already been discussed, or will be discussed elsewhere (van Riper and van Riper, this volume). Additional man-influenced changes such as grazing, clearing land for agriculture, burning, and lumbering (cow, plow, fire, and ax) also destroy or degrade habitat for many natives, but these effects are not the subject of this paper. Direct effects of alien animal depredations on native plants and ecosystems were discussed above, but not in the context of native animal habitat. This will be touched on here, largely in relation to native birds (Gagne and Christensen, this volume, address invertebrate habitat). Information is largely taken from Banko and Banko (n.d.), and the large volume of data collected by Scott et al. (in press) during the U.S. Fish and Wildlife Service Hawai'i Forest Bird Survey.

Effects of feral sheep and goats on nene habitat were judged important in local population impacts by Baldwin (1947). Cattle, goats, and possibly pigs were believed highly important factors in nene habitat degradation in the mid-1850's and later (Banko and Banko, n.d.). Effects begun then, together with invasion of alien plants, may have permanently altered considerable habitat.

Grazing by sheep and cattle was partly responsible eliminating, fragmenting, and degrading highelevation akiapola'au habitat (Scott et al., in Effects of feral sheep, goats, and mouflon on press). mamane habitat of the Federally endangered palila were serious enough to force a court order to remove the feral sheep and goats from Mauna Kea (Kobayashi 1979; Scowcroft 1983). Cattle grazing and lumber harvest on leeward Hawai'i severely affected habitat of 'akepa, Hawai'i creeper, and 'alala. According to Giffin, Scott, and Mountainspring (in prep.), nearly all of the undisturbed and none of the disturbed koa-'ohi'a forests in Kona were once occupied by crows. However, P.C. Banko (pers. comm.) has found breeding 'alala in koa-'ohi'a forests that were highly disturbed by cattle and other activities. Scott et al. (in press) said that cattle damage to forest understories on their Kohala study area on Hawai'i correlated with low densities of 'elepaio.

Feral ungulates were thought responsible for the lower 'amakihi densities in Maui dry forests than in similar dry forest habitat on Hawai'i. On Moloka'i, 'apapane are absent or present in low densities as a

result of deforestation by axis deer pigs, goats and cattle. On East Moloka'i, loss of 'amakihi is tied to axis deer depredations.

Feral pigs are important in the reduction of certain Hawaiian lobeliads, especially in wet forests (Diong 1983). Native birds that use these taxa include Bishop's 'o'o, Moho bishopi (if extant); the 'i'iwi; and the 'o'u (Scott et al., in press). Bishop's 'o'o may be especially sensitive to habitat degradation caused by pigs, partly because of lobeliad reduction. Pigs (and rats) also consume Freycinetia, favored by 'o'u and 'alala, and probably lower habitat quality of these birds accordingly.

Feral pigs may have negative effects on the Federally endangered <u>Pseudonestor</u> and <u>Melamprosops</u>. Both favor dense forest understories for foraging, and feral pigs are effective in simplifying understory composition and structure. Casey, Mountainspring and Scott (in prep.) showed that po'ouli habitat had "light pig damage and well developed herb, ground fern, and moss layers." They hypothesized destruction by pigs of microhabitat needed for land snails and other invertebrates favored by po'ouli.

Habitat degradation by feral pigs is also thought to affect Hawai'i creeper, 'akepa, and 'elepaio on Hawai'i; and Kaua'i thrush, small Kaua'i thrush, and the Kaua'i 'o'o on Kaua'i. Foraging of crested honey-creepers on Maui on understory nectar producers such as Rubus hawaiiensis when Metrosideros polymorpha blooms are scarce, may also be reduced by feral pig activity (Scott et al., in press).

The role of alien birds in degradation of habitat of native birds may be important. Peak populations of birds that invade forest ecosystems might affect foods (insects and plants) severely enough to permanently reduce habitat quality for natives. Such species as the Japanese white-eye, red-billed leiothrix, and common myna may have already reduced habitat quality by this means in many areas.

Indirect Effects

Impacts on other aliens. The important, and sometimes mutualistic, role of feral pigs in dispersing and encouraging weedy alien plants has been discussed previously. Mongooses, rats, and mice are also responsible for spreading alien plants, but the effects are less obvious and the magnitude uncertain. Alien birds disperse or are closely associated with numerous alien plants, of which Passiflora, Myrica, Schinus, Lantana, and Clidemia are probably the most important in native systems. Warshauer et al. (1983), Lewin (1971), and

Scott et al. (in press) noted associations of the following introduced birds with Passiflora: black francolin (Francolinus francolinus), Erckel's francolin (F. erckelii), gray francolin (F. pondicerianus), kalij pheasant (Lophura leucomelana), common peafowl (Pavo cristatus), wild turkey (Meleagris gallopavo), Leiothrix lutea, mockingbird (Mimus polyglottos), Japanese white-eye, northern cardinal (Cardinalis cardinalis), house finch (Carpodacus mexicanus), and spotted dove (Streptopelia chinensis). Fortunately, many of these species do not penetrate intact forest, but most will use forest openings created by man or feral animals for ingress.

A number of avian species in addition to those mentioned above are associated with alien grasses, herbs or shrubs (Scott et al., in press). They include California quail (Callipeopla californica), ring-necked pheasant (Phasianus colchicus), zebra dove (Geopelia striata), Eurasian skylark (Alauda arvensis) (a good indicator of degraded, fragmented forests), melodious laughing thrush, and nutmeg mannikin (Lonchura punctulata). Overall alien species diversity is highest in broken woodland and is heavily influenced by game bird occurrence. Cardinalis distributes Psidium spp. and Schinus terebinthifolius in lowland forests (Scott et al., in press). In a more subtle relationship among aliens, van Riper (1980) noted that alien birds might be contributing to the spread of naio (Myoporum sandwicense) on Mauna Kea through dispersal of seeds while feral sheep reduce competition from mamane through browsing.

Areas disturbed by feral ungulates contain a greater variety of alien bird species than undisturbed areas (Scott et al., in press). Stock pond and other water sources created by or for cattle are sought out by various game birds, house finches and common mynas, among others. Cattle and pig wallows also attract alien insect vectors of malaria or pox (van Riper and van Riper, this volume) that may thus reduce native bird populations. In some instances, continued presence of ungulates can perpetuate alien plants that would eventually give way to natives in their absence (Loope and Scowcroft, this volume). The establishment of alien plants after disturbance by feral animals, which are then able to maintain permanent populations in the absence of animals through allelopathy, monotypic stands, or altered nutrient cycles, has also been noted (Smith, this volume). The encouragement of introduced vegetation via alien animal distribution and cultivation contributes an alien fauna of snails, insects, spiders, other invertebrates, and plant pathogens (Howarth, this volume). Ecosystem modifications caused by the negative effects of these associated

aliens on native vertebrates and invertebrates could be

tremendous.

Forest openings do not always need to be caused by man or his associates to encourage alien birds. The apparently natural phenomenon in Hawaiian forests called 'ohi'a dieback (Mueller-Dombois, this volume) is correlated with reduced native and increased introduced birds. In scattered dieback sites in the Hamakua area of Hawai'i, 'apapane, 'i'iwi, 'oma'o, and 'elepaio numbers were 70, 77, 47, and 93% lower than in tall, closed canopy forest. Red-billed leiothrix and Japanese white-eye numbers were 30 and 34% higher (Scott et al., in press). Patchiness of vegetation of different sorts can favor native and non-native alike. For example, 'i'iwi and melodious laughing thrush both occur in greater numbers where understory diversity is high; native tree falls may help create such diversity (Scott et al., in press).

Nutrient cycling. Smith (this volume) stated that the effects of alien plants on nutrients in Hawaiian ecosystems deserve special consideration. The danger that aliens such as Myrica can, through nitrogen fixation, create their own favorable environment on Hawai'i's young and nitrogen-poor soils was emphasized. A study to determine the role of Myrica faya in altering primary succession in Hawai'i Volcanoes National Park has been proposed and funded (P.M. Vitousek, pers. comm.).

Feral pigs also play an important role in altering nutrient cycling in Hawaiian systems. They are distributors of Myrica faya, the berries of which average 12% of the total volume of food taken in the Puhimau Unit of Hawai'i Volcanoes National Park (n = 54 adults taken by hunting) on a year-long basis (C.P. Stone, unpubl. data). But probably more importantly, pigs in nitrogen-limited areas can also modify nutrient sinks, availability, and dynamics through their rooting activities. Where pigs are absent, organic material (and nutrients) build up (Higashino and Stone 1982) and ultimately affect soil formation. Where pigs root, the availability of "nitrogen [and other nutrients] to plants and the potential for nitrogen losses to the site (in leaching or denitrification) is greatly increased" (P.M. Vitousek, pers. comm.; Vitousek et al. 1979; Vitousek et al. 1981). Short-term nitrogen availability (favoring alien plant establishment) and long-term nitrogen loss (preventing the usual succession of natives) may be the pattern on such sites, especially if pig disturbance continues. Parent soil materials (ash, pahoehoe, or 'a'a) also affect nutrients, and the long-term advantages of nitrogen-fixers on some sites may not always hold as nutrient

availability changes (Vitousek, Van Cleve, and Bala-krishnan, in press). However, the continual influx of alien plant species is likely on pig-altered sites. The effects on plant and animal succession and community composition as a result of altered nutrient availability alone could be substantial. Pigs also alter ecosystem structure and processes through trampling, alien propagule introduction and enhancement, reproductive reduction of natives, and soil erosion, as noted Pig rooting and defecation favor alien soil altering nutrient cycling invertebrates, further (Howarth, this volume).

REDUCTION OF ALIEN IMPACTS

It should go without saying that extreme care must be exercised in the introduction and translocation of alien birds and mammals in Hawai'1. The best way to manage aliens is to prevent new species from entering the State and to prevent aliens that are present from affecting additional areas. As indicated in table 2, introductions that have recently succeeded are occurring at a much more rapid rate than introductions by either Polynesians or nature prior to man. The Hawai'i Department of Agriculture (DOA) and the Department of Land and Natural Resources (DLNR) have responsibility for controlling the introduction of vertebrates under Chapter 150A, Part II of Hawai'i Revised Statutes (HRS) and Chapter 187, Sect 1.2, HRS (Burr 1984). DOA administers Chapter 150A and maintains a list of prohibited entry species. It is expected to confiscate animals and charge the owners for expenses. DLNR administers Chapter 187, which covers translocation from one area in the State to another as well as importation. However, only the introductions proposed by DLNR are covered; other proposals are not addressed. If an animal escapes, it is classified as "wild" and a permit is required under Chapter 191 to control or eliminate it when it is involved in agricultural damage, is a nuisance, or is a health hazard (Burr 1984). The DLNR and DOA cooperate closely on updating the DOA list of restricted or prohibited entry species. There have been recommendations to develop a list of species that should be exempted from the wild bird protection provision.

Complexities of Damage Control
 "Ecology may not only be more complex than we think; it may be more complex than we can think" (F. Egler). Perhaps the major problem in understanding the true impacts of aliens and devising management strategies to reduce them is the number of confounded parameters involved. Before damage can be understood, predicted, and overcome, one may need to know how inter-actions occur among: soil fertility, weather, land use

Table 2. Successful colonizations of mammals and birds in Hawaii during different time periods.

			Historical Introductions (200 years)
	1.	3	18
Species	20,000,000	500	11
	20*	1	45
Species	1,000,000	1500	4
	Species	(20 million yrs) 1 Species 20,000,000 20*	Native Species Introductions (20 million yrs) (1500 years) 1 3 Species 20,000,000 500 20* 1

^{*} These underwent considerable adaptive radiation to form 35 extant species and many now extinct species (see Olson and James 1982).

history, plant phenology, predation, competition and other interrelationships with many species; population structure, density, distribution, and dynamics; animal movements, nutrition, and the vegetation complex. Such knowledge does not come cheaply or in a short time or from one study area, because problem vertebrates are long-lived, mobile, adaptable, and difficult to observe. Good information on one parameter, such as population density, may be misleading (Van Horne 1983). For example, high densities of young animals might be indicative of poor habitat, which is occupied by young because of social dominance by adults elsewhere, or because of high reproductive success and temporary survival. Attempting to reduce vulnerable problem animals in such situations might not be efficacious.

Other information required for good control programs includes the effects of different population levels upon the resource at risk, the cost of conducting the control, the value of the resource protected, effects of control on nontarget animals, effects of control on the resources being protected and on the ecosystem, the amount and length of followup needed, and feedback as to the effect on the problem animals. Managers need to establish long- and short-term priorities to determine what resources can be brought to bear on problem animals in different ecosystems and situations. To predict effectiveness of control under established time and budget constraints, animal populations and productivity should be compared (through responsive models) to determine the optimum efforts to achieve the desired reduction in damage. Proper monitoring of control effects necessitates systematic sampling of both animal populations and the resources that This should really be done pre and post they damage. control at a minimum.

The goal of reducing the effects of introduced vertebrates upon Hawaiian ecosystems is not accepted by everyone. Some believe that nothing can be done; others that it is too expensive and/or time consuming; and others consider that alien vertebrates add scientific, aesthetic, social, recreational, or even cultural and religious values that are more important than the values of native ecosystems. Studies of the importance of these values in the minds of Hawai'i's citizens, and of the economics involved, have not yet been made; however, most informed people (probably a distressingly small portion of any population!) would probably agree that preservation and management of native ecosystems in some areas is necessary and desirable. There is now overwhelming evidence that in Hawai'i this depends upon reduction or elimination of alien vertebrate impacts. To eliminate the adverse

ing the aliens, at least "temporarily." The fact that individual animals can't just be killed "temporarily" raises a conflict about the value of life. So a decision to reduce the adverse effects of alien vertebrates becomes a complicated economic, social, political, ethical, aesthetic, recreational, scientific, and land use decision. It also involves a worldwide, as well as a local, community of interest in Hawaiian ecosystems. Let's assume we have somehow made the decision to control alien vertebrates to benefit native Hawaiian ecosystems in some areas. Then what?

Depredations

"Good fences make good neighbors" (R. Frost). opposing land uses such as sustained yield recreational hunting and native ecosystem preservation and management are to be supported and perpetuated (and this seems realistic), feral unqulates must be excluded from some areas and perpetuated in others. Fence construction is costly and maintenance is continual, but there is no other way to sustain adjacent land uses with these opposing objectives. Programs in Hawai'i Volcanoes and Haleakala National Parks to reduce and eventually eliminate feral goats and pigs are examples of ungulate control programs that depend upon fences. The question of who should build and maintain fences deserves further discussion elsewhere, but in this case the Federal government is assuming the sole responsibility for perpetuating Hawai'1's native ecosystems.

Once fences are constructed, reduction of the animals by hunting, snaring, trapping, or poisoning is possible. Removal of live animals for use elsewhere is usually expensive and time consuming, requires a place to put the animals, generally costs more than it is worth biologically, and does not usually result in elimination of the all-important last animals that can quickly repopulate the area with offspring. There are, of course, political and social considerations. Drift fences may be used to restrict animal movements within fenced areas or to direct animals toward accessible areas for removal. Internal barriers consisting of combinations of fences and topographic features may be necessary to delimit areas from which animals can be effectively removed. Such areas should be large enough to reduce major fencing costs and avoid artificial paddock-like situations, but small enough to allow efficient elimination of animals with the resources available.

Public hunting may be used as a tool to reduce depredations of ungulates in some instances, but management by public hunting alone usually results in sustained yield. Hunting as a control method is most

effective where habitat is limited and accessible. Removal of sheep from Mauna Kea and goats and pigs from parts of Hawai'i Volcanoes National Park has taken an organized, sustained use of agency "shooters" in conjunction with public "hunters." Barrett and Stone (1983) found that the Deputy Ranger or Citizen Hunter Program active in Hawai'i Volcanoes since 1972 was not effective in reducing feral pig populations except in highly accessible areas (within 500 m of a road). The average removal rate by citizen hunters (percentage of estimated carrying capacity) was 3% of the adult pig population every 6 months; 30-40% should be removed if populations are to be reduced to extinction in a 3-5 year period. Through use of agency hunters and dogs, we have achieved an estimated removal rate (as of May 1984) of 25% in one rain forest unit and over 50% in a mesic forest (Stone and Taylor 1984).

The Hawai'i Department of Land and Natural Resources recognized the need to manage ungulates within native ecosystems in the Hawai'i Wildlife Plan (Hawai'i Division of Forestry and Wildlife 1983:63):

Where the presence of big game populations within sensitive native ecosystems is destructive, elimination can be accomplished through public or staff hunting opportunities.... Where the public hunting is inadequate in removing excess game animals, drives and trapping should be employed, but only as a last resort due to the high costs.... Feral pig, goat and sheep populations should be monitored and maintained at levels resulting in minimum damage to watersheds and native ecosystem protection and should be controlled by public hunting whenever possible.... In Natural Area Reserves, the objective should be to reduce feral game mammals to the lowest possible levels using public hunting.

When combined with fencing and critical evaluation, and if organized properly, such programs might keep some populations in check. However, in most valuable natural areas, the goal should be elimination of ungulates rather than sustained yield, even at low population levels. The potential for increase when even a few animals remain is large.

Control of depredating ungulates with chemical toxicants is a controversial and expensive proposition, but it deserves further consideration in Hawai'i, considering the magnitude of the problem and the scarcity

of secondary and non-target animals. No toxicants are currently registered for use with ungulates. Chemical use entails a complicated process of registration, classification, labeling, and certification under the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA) of 1974 and the Federal Environmental Pesticide Control Act of 1972, administered by the Environmental Protection Agency (EPA) (Hood 1978). Use of toxicants for pig control in remote areas in Hawai'i would probably necessitate registration under Section 24 of FIFRA, which provides that a state may register pesticides formulated for distribution and use within that state to meet special local needs, if the state is certified by EPA as capable of administering the Act. Alternative emergency provisions under Section 18 of FIFRA, or Experimental Use Permits (EUP) for chemical use also exist under more limited conditions of re-

search and/or area of application.

The use of chemicals is neither a panacea nor an environmental disaster. Chemicals can be used safely and effectively in some cases and can have certain advantages such as low cost (once registered), target species specificity, non-specificity within a population (all sexes and ages are vulnerable), and ease of use in remote areas. However, chemical effectiveness usually depends upon bait acceptance, and some animals may be difficult to attract to bait -- e.g. feral pigs (J. Hone, pers. comm.; R.H. Barrett, pers. comm.; C.P. Stone, unpubl. data). Chemicals, like other animal control tools, must be repeatedly used as long as reproducing animals remain. Complete reliance on chemicals, biocontrol, fences, hunting, or any one tool is unrealistic, but all appropriate control methods should be developed and improved for use where needed. Although registering a toxicant is costly, information gathered in responsible research/management programs will be useful in meeting eventual registration requirements. Toxicants will likely be needed to control some species in some situations (see discussion below).

A number of research/management emphases are essential in well-conducted depredation control programs, and considerable research information and continual feedback are usually necessary. Some idea of ungulate population size, sex, and age structure, reproductive rate, and distribution in the control unit is necessary to determine whether rate of removal is sufficient to effect reduction. Information on rate of removal should be continually recorded and compared with theoretical or known reproduction and mortality. Indexes to the population being removed and to the resources being damaged are required to determine progress and adjust control strategies. Supplemental information on animal movements through radio telemetry is useful in

improving and adjusting control strategies to changing animal behavior and densities. Data on food habits may also provide cues to vulnerability or shifting behavior patterns as control progresses.

Primary emphases in ungulate control programs should be:

- 1. The necessity for efforts lasting many years.
- Continual learning and feedback about success of control (monitoring).
- 3. Provision for sufficient resources to effect reduction.
- 4. The development of multiple methods to reduce animals.
- It is likely that what will work in one area at one population level will not be as useful under different conditions. To summarize alliteratively, multiples [years and methods], money, monitoring, and modification are keys to controlling depredations by ungulates in Hawai'i.

Predation

"Well, so much for the unicorns" [said Noah, standing over 2 carcasses]. "From now on all carnivores will be confined to C deck" ("The Far Side"). Some things just don't mix, and the best way to preserve one is to get rid of the other. It is generally true that when predators need to be "controlled" to preserve and manage native Hawaiian ecosystems, the best way is to kill them. Mongooses, cats, and rats simply cannot be effectively excluded or repelled or trapped and transplanted in most situations in the wild. Again, this is a controversial matter with many ramifications beyond the ecological, but let's assume we have opted for controlling predator impacts.

Predator damage may sometimes be controlled by trapping where the plant or animal to be protected is restricted in distribution. Examples are protection of dark-rumped petrels from mongooses, cats, and rats at breeding colonies (Simons 1983); protection of nene in release pens in backcountry situations (N. Santos, pers. comm.; H. Hoshide, pers. comm.); removal of mongooses around an 'alala nest (Giffin 1983); or protection of a group of rare trees from rats (C. Zimmer, Shooting and trapping have been effecpers. comm.). tive in removing cats from somewhat limited areas (e.g. 415 ha Jarvis Island) (Rauzon 1983), if enough manpower However, chemical toxicants are necesis available. sary in most cases where the resource to be protected from predators is dispersed over a large area or over time.

Several rodenticides have been registered for agricultural use and some laboratory and field work has

Woodside 1953; Kridler 1966; L. Pank, pers. comm.). Risk to other animals (nontarget hazards) and to animals that eat poisoned animals (secondary hazards) are minimal in Hawai'i, at least insofar as native species are concerned. Nevertheless, we need quantitative information about these hazards; about baiting techniques in native ecosystems (including bait spacing, timing, substrate, and doses); more lab research on toxicity levels, acceptance, and appropriate chemicals; and more information on predator ecology and potential for control in Hawai'i's ecosystems. Basic practical questions of feasibility in terms of reinvasion rates and sizes of areas that can be effectively treated in different situations are largely unaddressed.

A 3-year program headed by the U.S. Fish and Wildlife Service (FWS), with the National Park Service (NPS), and the Hawai'i Division of Forestry and Wild-life (DOFAW) cooperating, has been designed to develop a "drop-bait" toxicant to eliminate or reduce mongooses seasonally in nene and 'alala breeding areas, waterbird habitat, colonial nesting sites for seabirds, and perhaps native forest other than that used by crows. The objective is to obtain a special local need registration under Section 24 of FIFRA (J. Keith, pers. comm.). Current research on rat ecology and control in native forests is under way, with limited efforts in Haleakala and Hawai'i Volcanoes National Parks (Stone et al. 1984; C. Stone, unpubl. data). Funding for a more substantial program of rat and mongoose research may be available from NPS and could be coordinated with the mongoose project headed by FWS. The policy of the DLNR on small alien mammals as stated in the Hawai'i Wildlife Plan is to support research by others on predators and rodents; to implement control only when it is needed and will be effective; and to control only where cost/benefit ratios are favorable (Hawai'i Division of Forestry and Wildlife 1983).

Interspecific Competition

"New questions arise when many populations and entire biomes are being fragmented and reduced on such a scale and at such rates. These questions are a great challenge to the ingenuity of biologists Unless we solve them, we will end up with less than we intend, struggling in our ignorance to protect genetically eroding populations and decaying ecosystems" (T. Lovejoy). Despite a number of introductions of alien birds into Hawai'i in the last century (Moulton and Pimm 1983) and documented increases and extinctions of the species and populations involved (Banko and Banko, n.d.), we do not have good quantitative and qualitative information about adverse impacts of introduced birds on the native avifauna. Banko and Banko (n.d.) used an

historical/ecological approach to infer competition among different species and in different areas. If food habits of species pairs were similar and alien increases coincided in time with native decreases, competition was assumed to have played a role. Mountainspring and Scott (in press) and Conant (1981) examined densities of various species in different ecosystems at one point in time. Relationships between species pairs that were negative were assumed indicative of competition, and those that were positive, of association, for the purpose of using a common food base or other mutual resource. Variation in relationships with time of year or over a period of years was not considered.

Although both approaches have value, a full understanding of interspecific competition among native and introduced birds in Hawai'i awaits further study. Dynamic relationships throughout the year over a period of years need to be explored. Densities, reproductive rates, mortalities, and movements of potential competitors should be studied in relation to habitat variation (e.g. bloom or insect abundance, rainfall, temperature, population levels of other avian species, impacts of alien mammals, diseases, and other biota) over time. The effects on forest resources (especially during peak alien population levels) need to be determined and the permanence ascertained. Activity budgets, densities, food habits, and reproductive success of native birds in habitats with and without alien birds should be determined.

The potential for additional species of introduced birds to compete with native species still exists. Williams (1983a, b) suggested that red-vented bulbuls (Pycnonotus cafer) may have been deliberately released on O'ahu and on Hawai'i in 1966 and 1982, respectively. The red-whiskered bulbul (P. jacosus) was apparently accidentally released on O'ahu in about 1965. Neither species is noted for colonizing across open water, but both seem to be increasing on O'ahu and may disperse to neighbor islands (Williams 1983b; Conant 1983). Bulbuls are known to be rapid colonizers, agricultural pests, and potential threats to native forest birds. The possibility that these species and other introductions will further reduce forest invertebrates and plants must be taken seriously; initial populations should be removed where possible or closely monitored where not possible.

An important species such as the Japanese whiteeye or an irrupting species that cannot be controlled should be followed through introduction or buildup, population irruption, and population decline in several areas, and its impacts on forest resources, including native avian species, should be determined. Japanese white-eyes are currently widespread in native forests but may be declining or on the verge of doing so in some areas already (Dunmire, 1962). The possible increase of the Japanese white-eye and melodious laughing thrush in Kipahulu Valley (Scott et al., in press); the possible expansion of the laughing thrush at lower elevations in Ka'u and Kona; the decline of Leiothrix at low elevations especially on O'ahu (Shallenberger 1981); the close association of Leiothrix and the laughing thrush with increasing naio (van Riper 1980) on Mauna Kea; and the increase of Leiothrix on northwest Haleakala in Kula, are some areas of interest. We need a better understanding of the dynamics of alien bird populations in Hawai'i's forests. More information on rat population dynamics and behavior in different vegetation types, areas, seasons, and years is also needed, to better understand the importance of rats as competitors with the native avifauna.

In addition to better understanding the phenomenon of competition, we need to give further emphasis to the importance of large, intact areas in preserve design. As indicated by Scott et al. (in press), native birds need large undisturbed tracts of native forest to provide buffers against irruptions of alien birds and the perturbations caused by alien birds and mammals. Native invertebrates are also well served by intact native forests (Gagne and Christensen, this volume). Many introduced species in the past, and likely in the future, will be stopped near the forest edges unless there are roads, clearings, or trails into native for-Activities (including feral animal control) that open and fragment forests, thus enhancing further invasion of alien birds, invertebrates, and plants, need to be carefully evaluated. Optimum sizes of "alien resistant" tracts in different vegetation types should be determined. Vertebrates such as the melodious laughing thrush, Leiothrix, and Zosterops that do presently penetrate largely unmodified forests can have potentially devastating effects on native plant, invertebrate, and avian forms, at least during peak population phases.

Management-Research Coordination

"#!%?\$ Ivory tower research!" "#!%?\$ seat-of-thepants management!" (Subdued conversation between a natural resource manager and a researcher). In practice
we often take shortcuts in solving problems in natural
resource conservation. We don't have enough information, but we must begin to "do something." In acting
prematurely we risk making mistakes, but often the
problems are severe and call for immediate attention.
Waiting for more facts isn't good enough, especially
when they accumulate slowly. It is important that if
we are to manage without many of the facts needed,

however, that we proceed cautiously and learn from our Trial and error management of alien vertemistakes. brates must be designed to collect data on as many aspects of the ecology of damage as possible. Management efforts should be treated as experiments with replicates, controls, proper experimental design, statistical testing, and reporting (McNab 1983). Research personnel should be directly involved in coordinating with Management to increase the usable information from such "experiments." We cannot afford to further upset Hawai'i's badly disturbed native systems through improper and unquided management experiments. Nor can we afford to waste time in reinventing ineffective strategies and not taking advantage of the knowledge gained through considerable effort elsewhere. Continual and widespread communication of research and management findings is mandatory.

Multiple Approaches and Persistence

"There is no free lunch" (B. Commoner). This is especially true for those of us in Hawai'i who are concerned about managing disturbed and deteriorating ecosystems. History reveals no panaceas for reducing alien animal populations and impacts. Biocontrol, chemical toxicants, hunting, fences, and habitat improvement (for natives) are all useful tools, but all have characteristic disadvantages and varying degrees of impermanence (e.g. Howarth 1983). We need to know more about the entire arsenal of management tools, because different approaches are likely to be effective under different conditions. For example, we are changing feral goat and pig control methods in Hawai'i Volcanoes National Park as population distribution and densities and animal movements and wariness change. The ecological complexities touched upon above make the use of varied combinations of damage reduction methods necessary if management is to be effective. The current approach to damage control, called Integrated Pest Management (IPM), while more generally applied to invertebrates, recognizes that flexible approaches and multiple methods are usually needed to solve agricultural problems far less complicated than those we face Hawaiian ecosystems (Huffaker 1975; Wilson and Huffaker 1976; Flint and van den Bosch 1981; Ruggiero and Johnston 1984).

Control efforts must be coordinated at research, management, and administrative levels. Realistic long-term goals must be set and receive continued support to attain objectives. Planning and prioritizing for the future by research, management and administration must be carefully done on the basis of facts at hand, and should allow for the continued accumulation of better information and adjusting priorities as we learn. Long-term planning and persistent coordinated efforts

and support are essential if we are to reduce adverse

effects of alien animals on Hawaiian ecosystems.

TOWARD COOPERATIVE EFFORTS

"If you're not part of the solution, you're part of the problem" (Eldridge Cleaver/Bobby Seale). "We have met the enemy, and he is us" (Pogo). The problem of preserving and managing the remaining examples of Hawai'i's native ecosystems, especially through reduction and elimination of alien vertebrates, goes beyond what any one landowner, manager, or other special interest group (including conservationists) can accom-A local and international network of conservationists, developers or consumptive users, land use specialists, natural scientists, businessmen, educators, politicians, sociologists, economists, and other experts must be brought into the process of relating native ecosystems to community, national, and global The Nature Conservancy of Hawai'i has made concerns. considerable progress in this direction, although the initial focus was preservation and management of native bird habitat (a valid indicator for an initial action program), and the areas protected by The Conservancy are small and few, with budgets and staff to match (Holt and Fox, this volume). The State Natural Area Reserves System, now about 20 sites (P.Q. Tomich, pers. comm.), is also appropriate, but again, areas are small and few, and active on-site management is needed.

If the problem of alien animals in Hawai'i's exemplary ecosystems is to be dealt with effectively, a cooperative approach should be implemented. We will need to cooperatively choose important and representative ecosystems upon which to concentrate limited cooperative resources. Our choices should be based on considerations of preserve design, protection, and manage-We will need to decide which systems are most intact, most in need of preservation, and least likely to be influenced by aliens and other threats in the Increased communication among conservationists and developers would help both groups to better plan for the future. Zones of cooperation and buffer zones around protected areas should be seriously considered in planning (Gregg 1984). We will need to apply intensive, sustained, interdisciplinary research to protected and used areas alike, to understand the ecosystems we are dealing with in biological, socioeconomic, and other contexts. The ecology of aliens in systems managed for multiple use or sustained yield hunting deserves further study in this regard. We will need to know the consequences of periodic irruptions and declines of alien animals and the population biology of natives in protected and unprotected areas, and what governs the dynamics. We will need to fully understand the effects of our management actions on alien animals and on Hawai'i's ecosystems. We will need to explain the rationale and impacts of alien control programs to a wide variety of interested parties for a long time, and invite them to participate in decisions that affect them. We will have to seek a role in decisions made by others that impinge upon our responsiblity of managing protected areas through control of aliens to prevent degredation of ecosystems.

The tasks are enormously complicated, enduring, and time-consuming. Our knowledge of how to proceed, our progress in doing so, and even our communications about the problems involved (except within scientific/management circles), are rudimentary. But progress is being made, and the end result, reducing the impacts of aliens in Hawai'i's irreplaceable ecosystems, is well worth the effort.

ACKNOWLEDGEMENTS

I would like to thank C.W. Smith, L.L. Loope, J.M. Scott, P.K. Higashino, P.C. Banko, S. Mountainspring, J.D. Jacobi, R.L. Walker, F. Howarth, and P.Q. Tomich for reviewing the manuscript and for their helpful suggestions. J.M. Scott, W.L. Wagner, P.C. Banko, and W.E. Banko generously allowed me to adapt material from their unpublished papers elsewhere (including table 1 and the figure) for this paper, and I am grateful. Mahalo to S.M. Graves for drafting the figure. I am also indebted to D.B. Stone for encouragement, feedback, and typing and updating many versions of the manuscript on the microcomputer. I appreciate her patience, support, and judgement.

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