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IMPACTS OF ALIEN LAND ARTHROPODS AND MOLLUSKS ON NATIVE PLANTS AND ANIMALS IN HAWAI'I

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ABSTRACT

Over 2,000 alien arthropod species and about 30 alien non-marine mollusks are established in the wild in Hawai'i. While the data are too meager to assess fully the impacts of any of these organisms on the native biota, the documentation suggests several areas of critical concern. Alien species feed directly on native plants or their products, thus competing with native herbivores and affecting host plants. Alien predators and parasites critically reduce the populations of many native species and seriously deplete the food resources of native predators. Some immigrant species spread diseases that infect elements of the native biota. Others are toxic to native predators. There is also competition for other resources, such as nesting and resting sites. Even apparently innocuous introduced species may provide food for alien predators, thus keeping predator populations high with an attendant greater impact on native prey. Control measures targeted at alien pests may be hazardous to natives. Mitigative measures must be based on sound research and firmer understanding of the complex interactions and dynamics of functioning ecosystems. Strict quarantine procedures are cost effective in preventing or delaying the establishment of potential pests. Strict control or fumigation is needed for nonessential importations (such as cow chips, Christmas trees, and flowers in bulk). Improved review of introductions for biological control is required in order to prevent repeating past mistakes. Biocontrol introductions must be used only for bona fide pests and used in native ecosystems only in special circumstances. Sufficient funds must be committed at the time of any intentional introduction for long-term monitoring of its efficacy and environmental impacts. Mitigation of other novel perturbations (e.g. land clearing, grazing, rooting by feral pigs (*Sus scrofa*), and invading weeds) that favor alien invertebrates will also lessen their impacts.

INTRODUCTION

It is quite appropriate to discuss the impacts of alien organisms at a conference on the natural history of Hawai'i, since Hawai'i ranks as one of the prime areas of the world in numbers of established alien species. This is true for both plants and animals (both vertebrate and invertebrate groups) as well as for intentional and inadvertent man-aided introductions (Lewin and Holmes 1971). The reasons for this distinction are diverse, and much speculation has been offered in explanation. Since the ecological reasons for the invasion of Hawai'i provide background that helps one to understand the impact of introduced species, I will briefly review the phenomena of colonization and establishment of aliens.

This paper focuses on the impacts of alien invertebrates. Alien plants, vertebrates, and avian diseases are discussed elsewhere in this volume. However, it must be stressed that the impacts and ecological problems are interrelated. That is, it is often the mix of alien species acting in consort or sometimes competitively that disrupts native ecological processes. This relationship should become more clear from the examples.

This paper is further limited to the insects and certain other arthropods and to terrestrial mollusks, because there is at least some published information available. Not treated are several phyla of worms and other lower invertebrates and many smaller groups of arthropods. This is unfortunate, as earthworms, for example, play a major role in soil formation; yet we know very little of the earthworm fauna and its role, if any, in prehuman Hawai'i.

Even among the insects the task at hand seems overwhelming. To date over 2,000 species have become established in the wild in Hawai'i and perhaps 20-30 new arrivals establish each year (Davis and Chong 1968; Beardsley 1979). In contrast, approximately 30 species of non-marine mollusks have been established in Hawai'i. However, in some cases their impacts on the native species are better documented than for other invertebrate groups. There have been few studies of the impacts of alien invertebrates on the native biota. Most of the published accounts are anecdotal or relate to single observations. Still, patterns emerge from these examples, and inferences can be made.

The biota of the Hawaiian Islands evolved in splendid isolation. Only those few unusually vagile or lucky groups that were able to cross thousands of kilometers of ocean colonized the Islands. Many arthropods, and especially the insects, are experts at long-distance dispersal. Thus, it should not be surprising that insects and their relatives are the dominant consumers on oceanic islands, particularly Hawai'i.

CHARACTERISTICS OF COLONIZING SPECIES

In order to establish a successful breeding population, a colonizing species must be pre-adapted genetically to exploit the resources in the new land. Potential hosts must be present in enough numbers and in the right developmental stage; nesting and roosting sites, reproductive cues, and other ecological requirements of the species must also be present; and climate, including properly cued seasonal changes, must fit the development of the colonizing species. Since the chances of both sexes being introduced simultaneously are low and the vagaries of finding a mate in the new land are high, hermaphroditic and parthenogenetic species have a much better chance of becoming established than do dioecious species (Howarth and Moore 1983). Indeed, a high proportion of alien invertebrates in Hawai'i can use one of the former types of reproductive strategies. It also follows that generalist species establish more easily than specialists, since the former, with their wider host or prey ranges, are more likely to find suitable food. The genetics related to colonizing ability and host specificity are becoming better understood, and this understanding leads to management and control recommendations (Carson and Ohta 1981; Templeton 1979; Schonewald-Cox, this volume).

Competition with already established species is important but not primary in determining whether a particular species establishes or not. That is, species packing (the number of species that can share or exploit a given resource) is a separate phenomenon from the establishment of a colonizing species. One of the outcomes of the Hawai'i International Biological Program (IBP) studies was the realization that, as more species become established in a habitat, it becomes more probable that additional species will find a suitable niche; thus, the chance of an alien species being able to establish is directly proportional to the number of species already present rather than inversely proportional, as is usually assumed (Mueller-Dombois and Howarth 1981).

A newly establishing species, however, often creates vacant niches within an ecosystem in that it or its products may not be initially exploited by the resident species. In time, either some resident species will adapt to exploit the alien, or other aliens will arrive to exploit it (Southwood 1960; Strong 1979;

Conner et al. 1980). This process is occurring in many lowland, man-disturbed habitats in Hawai'i, wherein the establishment of alien species is enhanced by the disturbance caused by humans or by introduced organisms. Each new alien further improves the chances of colonization by yet additional species.

Over one-third of the alien invertebrates in Hawai'i were intentionally introduced, mostly for potential control of pest species, but also for pollination, food, and other natural products. The rest were inadvertent introductions. These are the hitchhikers taking advantage of the improving human transportation facilities.

IMPACTS OF ALIEN INVERTEBRATES

Given the major role of invertebrates, especially insects, in nutrient cycling in natural ecosystems, especially those of oceanic islands, it seems axiomatic that alien invertebrates have the potential to cause serious disruptions. Our knowledge of island ecology is still insufficient to fully assess the effects of any alien species on the native biota. However, the meager data do indicate the magnitude of the problem. Alien invertebrates have invaded nearly every habitat so far studied in Hawai'i from the seacoast to the tops of the tallest mountains, and they affect every trophic level. Partial analyses of the invasion and role of alien species in 2 native Hawaiian ecosystems, the montane rain forest and caves, were presented in the IBP studies by Mueller-Dombois, Bridges, and Carson (1981). In this paper, the potential negative impacts of alien species will be described and illustrated with a few examples. Many of the examples must come from outside Hawai'i, since more research data are available there.

It may be too late to distinguish specific effects of aliens in many of the man-disturbed ecosystems in Hawai'i. Man is best adapted to the drier lowland coastal zone, and most of the plants and animals purposely brought in for food or other applications are, as would be expected, also adapted to this zone. These are the habitats most disturbed by man and his introductions; thus, as explained above, still further colonization of these areas is enhanced. This is also the zone in which new arrivals first find themselves on disembarking from planes or ships. Therefore, only species able to cope with climate and disturbance in port environs are likely to establish.

Direct Consumption of Native Plants

A large number of alien insects will feed on endemic plant species, sometimes doing extensive damage or causing severe defoliation. In most cases the plants recover, and the longer term effects remain unstudied or poorly known. Certainly, however, widespread defoliation or decrease in productivity of structurally dominant forest tree species, such as defoliation of mamane (Sophora chrysophylla) by the moth Uresiphita polygonalis (Conant 1975), and the effect on koa (Acacia koa) of the plant louse Psylla uncatoides (Leeper and Beardsley 1973), represent serious perturbations not only to the trees and their associated fauna and flora but also in hydrology, agronomy, nutrient cycling, etc.

Adults of the Chinese rose beetle (Adoretus sinicus) often congregate on favored hosts and characteristically create large rectangular holes in the leaves. Certain native plants are especially attractive and are jeopardized by depredations of this beetle, e.g. the proposed endangered Hibiscadelphus distans and Abutilon menziesii (Wagner, Herbst, and Yee, this volume).

Some generalist feeders, especially colonial or social species such as aphids, whiteflies, scale insects, and termites, may be reducing the ranges of certain native plants, but hard data are lacking in most cases. These abundant species contribute to the demise of the native lowland flora; the survivors from the human disturbance of fires, grazing, urbanization, agriculture, and competition from alien flora must also withstand an onslaught of alien phytophagous invertebrates building up populations on alien hosts.

Alien insect species are implicated as important factors in the decline and endangerment of a few plants. The black twig borer, Xylosandrus compactus, a tiny black ambrosia beetle (family Scolytidae) with an extremely wide host range, burrows into the growing tips and twigs of the host and introduces the pathogenic ambrosia fungus Fusarium solani, thereby severely pruning the host tree and often killing major branches or the whole tree (Hara and Beardsley 1979). Among its hosts in Hawai'i, of which 108 species in 44 families are known (Hara and Beardsley 1979), are several rare native species including Charpentiera sp., Claoxylon sandwicense, Drypetes phyllanthoides, Cryptocarya oahuensis, Alectryon sp., and Santalum freycinetianum. Gagne (1971) considered the borer to be the most important threat to the monarch of Hawaiian forests, Drypetes phyllanthoides; and Wagner, Herbst, and Yee (this volume) listed it among major factors in the endangerment of Gardenia brighamii and Mezoneuron kavaiense.

The black stink bug, Comptosoma xanthogramma (White), was first recorded in Hawai'i in 1966 and quickly threatened to become a serious pest of legumes, especially in the lowlands (Beardsley and Fluker 1967). During its initial J-shaped population curve in the decade following its arrival, it decimated the rare 'ohai, Sesbanea tomentosa.

Another example is the solanaceous treehopper Antianthe expansa, which was discovered on O'ahu in mid 1971. Its populations exploded on various cultivated and wild solanaceous hosts. By 1975 it was known from all the main Hawaiian Islands. High populations often killed susceptible hosts. Feeding records on native Solanaceae are lacking; however, alien species that have such wide host ranges within a plant family and that are able to build up large populations on alien weeds, are potentially serious threats to related native plants.

Among the alien mollusks, the slug Milax gagates is widespread and abundant in montane habitats. Gagne (1983) reported it feeding on greenswords (Argyroxiphium spp.) at 1,860 m in Haleakala National Park and felt that it was an important attractant, inducing rooting by feral pigs (Sus scrofa) in the fragile montane bogs. F.R. Warshauer (pers. comm.) considered slugs a serious threat to native ground orchids.

The attrition of the lowland populations of Acacia koa is augmented by the Formosan subterranean termite Coptotermes formosanus, which severely weakens older trees and shrubs. Since seed production in koa is being limited by predation by alien invertebrates and its seedlings are being defoliated by alien Lepidoptera and other herbivores, most of these fallen trees are not being replaced in the lowlands.

Significant direct interspecific competition for host plants should be most severe when food resources are limited. Many native insects are highly host specific and also may have quite restricted ranges. As their hosts decline due to a variety of environmental impacts, not the least of which are depredations of alien invertebrates, the native herbivores also decline. The currently listed endangered plants probably have already lost much of their associated arthropod fauna.

For example, in a status report on native moths, Gagne and Howarth (in press) regarded loss of host plant a major factor in the extinction of 5 species of Macrolepidoptera including Hedylepta asaphombra on Joinvillea ascendens, Genophantis leahi on Euphorbia, and the large hawkmoth Manduca blackburni on Solanaceae. The larvae (where known) of the curious endemic scythridid genus Mapsidius are restricted to the declining and localized populations of Charpentiera spp. (Gagne and Howarth, in press).

Interference with Native Plant Reproduction

Seed predation may limit reproductive success of plants and thereby limit their distribution. In addition to the many native arthropods that are highly successful seed predators on native plants, there are in Hawai'i numerous alien groups that also specialize in seed predation. Some of these may directly compete with native seed feeders on some hosts, but their primary threat is the prevention of, or severe reduction in, reproductive success of the host.

Acacia koa in drier areas appears to be limited in this way and may die out in such habitats. Predators may destroy over 85% of the seed production in koa, and in some (especially drier) habitats, koa reproduction is now almost never by seed (Stein 1983). Many ant species are also effective seed and seed sprout predators (Bond and Slingsby 1984).

Plants have evolved a variety of strategies to exploit local biotic or abiotic dispersal agents to move pollen from the anther to the stigma. The degree of outcrossing is important in maintaining variability and genetic fitness. The fact that a higher percentage of the Hawaiian flora has obligate outcrossing mechanisms compared with continental floras (Carlquist 1974) indicates a relatively greater reliance on indigenous pollinating mechanisms. Unfortunately, little work has been done on pollination biology among Hawaiian plants, although the role of birds has received some attention. Among the total native insect fauna there are perhaps a thousand species that habitually visit flowers and are potential pollinators. Many of these, including the yellow-faced bees, Hylaeaus spp., and a great many moths, flies, beetles, and wasps, probably coevolved with elements of the flora to form mutualistic relationships.

Alien invertebrates have disrupted these pollination systems in several ways:

1. Changing the pattern of outcrossing among plant species, leading to a possible decrease in fitness or hybridization with relatives.
2. Theft of nectar from the plant, thus reducing the chance of pollination by legitimate visitors.
3. Reduction or extinction of coevolved pollinators leading to the decline of the plant cohort dependent on them.
4. Interspecific competition among pollinators for nectar resource, leading to the decline of the native species.

Foraging behavior among pollinators can be viewed as a dynamic strategy in which the caloric cost of foraging must be offset by the calories gained. Because pollination is important to agriculture, much research has been focused on modeling this energy equation. Different pollinator species may use widely different strategies to maximize their energy returns. Plants exploit these differences by adapting flower morphology and nectar production and composition in space and time to attract species that fit their own reproductive strategies. The parameters involved include foraging ranges, number of flowers visited per trip, floral constancy, genetic outcrossing, climatic limits, nectar composition, and competitive behavior.

The most important introduced invertebrate pollinator is, of course, the European honey bee, Apis mellifera. This species was purposely brought to Hawai'i about 1875 as a honey producer and pollinator. It quickly naturalized in native and alien habitats from the sea coast to near the tree line. Its large sophisticated colony confers on it a foraging strategy very different from that of any of the native pollinators; it seems likely that it has disrupted the natural reproductive patterns of many native plant species, but there are no data to support or refute this. Honey bee colonies are very efficient at exploiting high quality resources such as a tree with massive blooming. Scouts locate nectar sources and return to the hive to recruit foragers which concentrate on that source until it is exhausted. Thus, for some massively blooming trees, outcrossings may be reduced. On the other hand, the large colony, exchange of pollen among workers, the wide ranging foraging, and the catholic (generalist) tastes of the bees mean that pollen from quite varied genetic sources may be carried by Apis workers (Roubik and Buchman 1984). Perhaps some of the hybrid swarms now seen among native floral groups are the result of indiscriminate outcrossing pollination.

In Central America, low colony densities of the alien Apis mellifera did not appear to adversely reduce the colony vigor of several sympatric native social bees, even though there was considerable overlap in plant species visited. Many of the foraging strategies employed by both the native bees and the honey bee probably developed through intercolony competition (Roubik 1983). Curiously, in Central America the honey bee is able to exploit many native plants (Roubik 1983), whereas in New Zealand this species forages predominantly on introduced plants (Donovan 1980). In Central America there are many native social bee species, and many of the floral taxa have coevolved to exploit the foraging behavior of colonial species. In contrast, New Zealand has a diverse assemblage of primitive solitary bees only, and the native flora evolved without the influence of colonial pollinators. Hawai'i is similar to New Zealand in that there is only one native group of solitary bees, albeit a speciose one with more than 60 known species.

One big competitive advantage of social species like the honey bee over most other pollinators, including birds and other bee species, is that large honey stores permit them to wait out bad times and rapidly recruit foragers to exploit newly developing resources (Roubik and Buchman 1984).

Little is known of the potential impacts of other alien pollinators. The 4-5 alien bee species besides the honey bee are generally lowland, open-habitat species and probably mostly associate with alien plant species. The large carpenter bee Xylocopa sonorina aggressively robs nectar from many sympetalate flowers (Gerling 1983). Mostly introduced ornamentals are affected, but some lowland native populations of Hibiscus, Ipomea, and others may also be attacked. Not only are robbed flowers less likely to be pollinated, but such flowers and the plant are less likely to be visited by legitimate pollinators.

Ants, particularly Pheidole megacephala, are also notorious nectar robbers. Their aggressive defense of food sources acts to deter other species from using the flower. Many plants have evolved a variety of defenses, such as hirsute stems, in order to reduce loss from ants and other robbers. Ants were not part of the native fauna, and some native plants may be quite vulnerable to their impact.

Although direct competition among alien and native pollinators may reduce populations of some natives, the indirect results of habitat loss (particularly nesting sites) and predation on native pollinators by alien invertebrates have reduced their numbers even further. At the same time, with the loss of such a large percentage of the native plant cover from lowland habitats (Wagner, Herbst, and Yee, this volume), many coevolved systems have been interrupted, i.e. either the plant or the pollinator species populations became too low to maintain the other, and one or both became extinct. The endemic yellow-faced bees appear to be greatly reduced in both species and numbers of individuals from Perkins' day (Perkins 1913).

Predation and Parasitism of Native Animals

A large proportion of alien invertebrates is predaceous or parasitic. Two principal factors are responsible. First, generalist species in the higher trophic levels often become established more easily than other guilds (Mueller-Dombois and Howarth 1981), and therefore a relatively high number of predators and parasites are characteristic of island faunas (Janzen 1973). Secondly, the popularity of purposeful introductions for biological control resulted in a large number of entomophagous species being imported and released.

Alien predators and parasites have had disastrous impacts on native organisms (Zimmerman 1948, 1958; Solem 1976; Wells, Pyle, and Collins 1983; Howarth 1983; Gagne and Howarth in press), but space allows only a few better documented examples to be given here. The environmental risks present in biocontrol introductions were reviewed by Howarth (1983), Pimentel et al. (in press), and Gagne and Howarth (in press). These will be discussed below. More species extinctions can be attributed to the impact of species imported for biocontrol than can be attributed to the much more maligned chemical control (see also Honneger 1981; Pyle, Bentzien, and Opler 1981; Clarke, Murray, and Johnson 1984).

Of the alien invertebrate predators, ants, particularly the big-headed ant, are the most notorious and have been most implicated in the extinction of native species in Hawai'i (Zimmerman 1948; Solem 1976; Gagne 1979; Hardy 1981). Even though there have been few controlled studies on their impacts on native ecosystems, the circumstantial evidence is clearly incriminating. All of the 35-40 species of ants currently established in Hawai'i are alien, and most of them are distributed mainly in lowland tropical or disturbed open habitats (Huddleston and Fluker 1968). Most are also cryptic, nocturnal, and nest in soil or wood cavities; therefore, their biologies and impacts remain poorly known. Several species are common and widespread and may become locally dominant (Huddleston and Fluker 1968). However, it is the aggressive species with larger colonies that have the most potential for harm. In Hawai'i these include the big-headed ant, Argentine ant (*Iridomyrmex humilis*), long-legged ant (*Anoplolepis longipes*), and the fire ants (*Solenopsis geminata* and *S.* sp. "A") (Huddleston and Fluker 1968). *I. humilis* and *A. longipes* have not yet reached their full potential range in Hawai'i and pose grave threats to the native fauna (Hardy 1981; Fellers and Fellers 1983).

Social predators are not present in the native fauna, and wherever these aggressive ants are common, nearly all of the exposed, naive native arthropods are threatened, as the native fauna evolved in the absence of such a foraging style and is now vulnerable. Gagne (1979), in his study of arthropods associated with 'ohi'a (_Metrosideros polymorpha_), found only species resistant to ant predation in areas where ants were common. Among native species were gall makers, borers, vagile species able to escape, and those with repugnatorial scent glands. Flightless native species, particularly predators, are believed to be most vulnerable (Zimmerman 1948; Fellers and Fellers 1983; Hardy and Delfinado 1974). Ants can competitively exclude some predators by efficiently consuming most of their prey (Risch and Carrol 1982; Lubin 1984). Perkins (1913) noted the near absence of native arthropods, especially beetles, where ants were numerous. Solem (1976) felt that ant predation was a major factor in the extinction of Hawai'i's endemic endodontid land snails.

Ants feed primarily on food rich in energy or proteins, such as honeydew, nectar, seeds, live prey, and carrion. Their colonial lifestyle with chemical communication allows rapid recruitment at and exploitation of high density food resources. Workers continue to gather food even though physiologically satiated (Risch and Carrol 1982), and excess food is stored in the colony (usually as increased brood). If food supply wanes, the brood is cannibalized. In this way the colony can withstand tremendous fluctuations in food supply.

The impacts of ants on animal populations are far greater than would be predicted from the number of prey consumed, since worker numbers and pugnacious behavior discourage other organisms from foraging, feeding, or roosting in ant-infested areas. Disruption of pollination has already been mentioned. Other examples are prevention of parasitism and predation of honeydew-producing homopterans, discouragement of feeding of herbivores, and disturbance of small animals from their hiding places. In the Galapagos, Lubin (1984) found that the alien little fire ant, _Wasmania auropunctata_, was able to displace and extirpate not only several other ant species, including the endemics, but also several spiders and a scorpion.

Recently 2 species of vespid wasps, the yellowjackets, also social predators with large colonies, entered Hawai'i. Both are temperate zone forest species that have extremely catholic tastes. Unfortunately, they pose a grave threat for many native species living in upland forests. Underscoring the importance of genetic makeup to the success of colonizing species, one of these wasps, _Vespula vulgaris_, is a boreal species and generally prefers coniferous forests. It also appears to have a strong seasonally controlled diapause and is only weakly established in Hawai'i. The other species, _V. pensylvanica_, is much more plastic and has been able to invade upland mesic forests and alpine scrub. The problem race of V. pensylvanica was first reported in 1977 and subsequently rapidly spread throughout the islands (Nakahara 1980). Its J-shaped population curve corresponded to an alarming decline in several native groups, notably Drosophila (Wells, Pyle and Collins 1983; H.L. Carson, pers. comm.), and Lepidoptera (S.M. Gon, III and W.P. Mull, pers. comm.). The huge colonies, sometimes a meter or more in diameter, represent significant numbers of consumed prey.

V. pensylvanica is currently in decline or stable in most areas, suggesting that food may have become limiting (i.e., the more naive prey are now so low in numbers as not to support as large a population of wasps) or that other intrinsic or extrinsic factors are limiting their populations. The indirect impacts on other predators, notably the native forest birds, were apparently not studied during the wasp's high population phase. Breeding success in passerines is generally related to availability of suitable prey items, which for the native species include caterpillars and other arthropods known to be prey of Vespula. The aggressive stinging behavior of the wasp may also have affected naive native animals. The native solitary diurnal predatory wasps, e.g. Odynerus spp. and Ectemnius spp., which share many prey species with Vespula, also would be expected to be severely affected.

Zimmerman (1958) lamented the loss of Hawai'i's moth fauna thusly: "The importation of parasites to control various moths of economic importance, together with the accidental importation of other parasites has resulted in wholesale slaughter and near or complete extermination of countless species. It is now impossible to see the Hawaiian Lepidoptera in the natural proliferation of species and individuals of Perkins' day. Many are forever lost." Zimmerman (1948) also believed that the reduction of native caterpillars led to the rarity and perhaps extinction of native predators, especially Odynerus wasps.

Since the mid 1950's 3 predatory snails (Gonaxis kibweziensis, G. quadrilateralis, and Euglandina rosea) have been introduced into Hawai'i in hopes of reducing populations of the pestiferous giant African snail (Achatina fulica). Of these, E. rosea has been most seriously implicated in the extinction of many native tree snails including the endangered genus Achatinella. Hadfield and Mountain (1981) presented good evidence demonstrating that the demise and complete extirpation of a well-studied population of Achatinella mustelina coincided with the arrival and multiplication of E. rosea in their study site. Their study confirms the circumstantial evidence and dire predictions made by van der Schalie (1969) and others.

Unfortunately, the same scenario is being replayed on other Pacific Islands as these predatory snails are still being spread purposefully by well-intentioned but misinformed individuals who hope to control the giant African snail (Wells, Pyle, and Collins 1983; Tillier and Clarke 1983; Clarke, Murray, and Johnson 1984). These introductions continue even though the efficacy of E. rosea for the control of populations of A. fulica has not been rigorously demonstrated. For example, populations of A. fulica often decline in the absence of E. rosea (Mead 1961, 1979; Tillier and Clarke 1983; Christensen 1984; Clarke, Murray, and Johnson 1984).

Populations of native tree snails appear to be strongly negatively correlated with populations of the alien garlic snail, Oxychilus alliarius, in many habitats on Maui (Severns 1984). This species is apparently an omnivore and opportunistic predator, and sometimes reaches incredible populations in forest leaf litter.

Birds and their nests harbor a large and diverse assemblage of parasitic and nidicolous invertebrates. Several of the alien species in Hawai'i potentially are important blood sucking parasites on native birds, but studies are few. Goff (1980b) found the northern fowl mite, Ornithonyssus sylviarum, on the house finch (Carpodacus mexicanus) in Hawai'i Volcanoes National Park. Besides their potential for disease transmission among native forest birds, this and related species, especially the tropical fowl mite, O. bursa, and the chicken mite, Dermanyssus gallinae, are known to decrease vigor and disrupt fledging success in their hosts by exsanguination.

Transmission of Disease Organisms Among Native Biota

Alien invertebrates, especially mosquitoes, that transmit avian diseases among naive native birds are considered to be among the more serious threats to the survival of some species. This is one of the better documented impacts of alien invertebrates on native species (see van Riper and van Riper, this volume), but further studies are needed.

Alien invertebrates also vector plant diseases, and some of these pose serious threats to native flora. The black twig borer's role in transmitting a pathogenic fungus has already been described above. The demise of the American elm (Ulmus americana) as a result of the Dutch elm disease spread by related beetles in North America shows that this problem is not confined to islands. The alien koa psyllid Psylla uncatoides was incriminated by Leeper and Beardsley (1973) in the mechanical transmission of native koa rusts, Uromyces spp., on Acacia koa and the potentially endangered A. koaia. Here is an example of a native group of diseases that appears to have become more virulent on native hosts when a more efficient vector became established. However, much of the dieback of the host trees was attributed to the feeding injury of the psyllid rather than to the rusts (Leeper and Beardsley 1977).

Insects and plant-feeding mites are particularly well adapted to transmitting a great variety of plant diseases, and much work has been done on their role in agricultural systems. Very little has been done in natural systems in Hawai'i, but a relatively large number of alien arthropods, such as aphids, leaf-hoppers, true bugs, and mites, belong to groups known to be efficient vectors.

Alien invertebrates may harbor alien diseases and act as carriers or reservoir hosts, i.e. tiny "Typhoid Marys", facilitating the spread of these diseases among susceptible hosts. The problem is poorly researched in Hawai'i, but may account for the disappearance of certain native groups. Native crayfishes (Astacidae) in Europe are being extirpated and driven to the brink of extinction by the fungus disease caused by Aphanomyces astaci, and disseminated by the introduced North American crayfishes Procambarus clarkii and Pacifastacus leniusulus. Both native and alien crayfishes are susceptible, but a higher percentage of aliens survives. Some of the survivors become resistant and act as reservoirs or carriers for new epizootics. Given the high reproductive rate of the alien species and their higher survival rate from this alien disease, the alien species become more and more numerous at the expense of native species after each epizootic phase and each generation (Wells, Pyle, and Collins 1983).

A similar process may be occurring here in the leaf litter with the alien sandhopper Talitroides topitotum and the native talitrid sandhoppers. T. topitotum has nearly replaced native species in the leaf litter in most areas below 1,000 m in Hawai'i. In New Zealand where T. topitotum is still spreading, it is also replacing the native species, apparently in large part by the interaction of an alien milky disease and amphipod populations (K.W. Duncan, pers. comm.). A similar milky disease is present in T. topitotum in Hawai'i.

Mead (1961, 1979) postulated from field observations in Hawai'i that a bacterium, Aeromonas sp., was the main factor controlling populations of the giant African snail. The rat lungworm Angiostrongylus cantonensis also is known to infect a broad range of snails. These diseases could be a factor in the decline of native snails.

Synergistic Effects among Aliens

Often 2 or more harmful alien species may act in consort so that their joint impact is more severe than that of the several species acting separately. Even an otherwise innocuous or seemingly beneficial alien may, in fact, act in consort with other aliens with a consequent synergistic effect, causing great harm to the native biota.

Alien invertebrates may be food resources for alien predators, may pollinate alien plants, may disperse alien plant propagules, may tend and disperse alien herbivores, and may alter soil structure. All of these activities will tend to favor certain alien species at the expense of natives. In the more disturbed habitats where large numbers of aliens have become established, many if not most of the ecological processes within the community are now carried out by aliens. Without intensive artificial management, native species are at a great disadvantage in these areas.

Many pestiferous ant species tend alien honeydew-producing homopterans, such as aphids, mealy bugs, and treehoppers. Nearly 50 species of potentially pestiferous honeydew producers have become established. Many are host specific and mainly attack alien plants. Others are more catholic feeders and are important herbivores feeding on native species. Many of these alien honeydew producers require mutualistic ants for efficiently protecting them from predators and dispersing them from plant to plant. The ants gain from them an abundant food supply, and, in fact, some of the most pestiferous ant species would possibly not have become established had not suitable honeydew-producing species already been present. Furthermore, the ants in general might not have become such a problem to native species had they not been able to exploit these plant-sucking bugs. It may be that the ranges of some alien ant species are restricted at present because of the absence or rarity of suitable honeydew-producing species in certain areas.

Another case of synergism exists among scarab dung beetles, mongooses (Herpestes auropunctatus) and cattle. Several scarabs were intentionally introduced to remove cow dung from pastures, thereby allowing grasses to regenerate and reducing the larval food of the horn fly (Haematobia irritans), a pest of cattle. Not only do the beetles thus favor invasion of Hawaiian ecosystems by cattle, they also are an important food source for the mongoose, especially in upland pastures. In fact, the mongoose might not maintain high populations in pastures and neighboring areas without the dung beetles (Tomich 1969). Pimentel et al. (in press) thought that the mongoose actually favors the population of the roof rat (Rattus rattus) in Puerto Rico by reducing its ground-dwelling competitor, the Norway rat (R. norvegicus).

Alien invertebrates are important pollinators of alien plants, including weeds. The honey bee probably plays an important role in successful seed set for a great many alien species, including some weeds. Several species of the obligate, specific pollinators of fig trees, including potential weed species, were intentionally introduced. These never would have escaped from cultivation had their specific wasp pollinators not been introduced. One of the major reasons more of the thousands of alien species of orchids and other ornamental plants have not escaped cultivation is that their specific pollinators have not become established. If an effective pollinator is introduced, the pollinated plants might escape cultivation and become a problem in native ecosystems.

A few higher plants are dispersed by arthropods, and ants are the most important agents. The role of myrmecochory (seed dispersal by ants) in the distribution of weedy aliens deserves more study. Hawai'i has no native ants, and thus is not expected to have ant-dispersed plants among the native flora. In South Africa the alien Argentine ant (a species also alien in Hawai'i) is disrupting the seed dispersal of several native myrmecochorous plants and may eventually cause their extinction (Bond and Slingsby 1984).

Alteration in Soil Formation and Structure

Invertebrates, especially earthworms, play a major role in soil formation and structure. Unfortunately, I have not been able to review the impacts of alien earthworms, nor is there much information on the role of native soil organisms. Colonial soil insects, such as termites and ants, greatly alter the soil in the vicinity of their nests, and few plants (possibly all of them aliens) thrive in such areas.

Termites greatly increase the breakdown rate of woody material and thus may make some plant nutrients less available to native species. The role of dung beetles (and other alien dung feeders) in cleaning up cow feces has already been mentioned. Few native invertebrates can exploit the dung of alien vertebrates. The incredible populations achieved by some alien invertebrates in certain habitats, e.g. isopods, millipedes, the garlic snail, and some ants, represent significant changes in the nutrient cycling process even if their direct impacts are obscure.

Hybridization with Related Native Forms

If the alien has a close relative among the native fauna, hybridization is possible, with the possible swamping and eventual extinction of the island species (Wells, Pyle, and Collins 1983). Hardwick (1965) presented morphological evidence that the alien corn earworm Helicoverpa zea population on Laysan Island may have introgressed with an undescribed native species. He also believed that the apparent extinction of the related endemic species H. confusa from the main Hawaiian Islands may have been due to aggressive males of H. zea becoming locked in copula during attempts to mate with H. confusa females. Under this scenario an increasingly larger percentage of H. confusa females would have been removed from the population with each generation.

Effects of Alien Pest Control

Finally, alien invertebrates interfere with human endeavors in the Islands. This competition often leads to chemical and biological control procedures. Chemical applications also may kill native species and pollute the ground and water resources, impacting native species living there. Biocontrol introductions sometimes also attack native species. Perhaps the most notorious examples are the alien fruit flies. These pests have provoked proposals of massive eradication schemes, some of which have been attempted, including intensive aerial spraying of large parts of the island of Lana'i with broad-spectrum pesticides. In addition, over 2 dozen species of predators and parasites, some of which now attack native arthropods, have been introduced.

Control of alien pestiferous mosquitoes has included draining and chemically treating wetlands, with attendant environmental problems, as well as the introduction of mosquito fishes (Gambusia spp.) to numerous water bodies in the State. This spread of predatory fishes continues today even into remote areas, despite the fact that these generalist predators are known to severely disrupt native aquatic life (Haas and Pal 1984), including extirpating the rare damselfly Megalagrion pacificum from many areas (Moore and Gagne 1982).

SOLUTIONS

With so many alien species established in Hawai'i and their impacts so pervasive, the initial reaction is to throw up one's hands and say that we are too late to save much of Hawai'i's biota. However, native species display a resilience in the face of these new destructive forces, and many spectacular natives still survive, a fact that is stressed in other papers in this Symposium. Such recent biological discoveries in

Hawai'i as the cave and aeolian ecosystems, raptorial predatory caterpillars, hundreds of new species of arthropods, a new extant bird species, and new information on the evolutionary biology of Drosophila, should instill new conviction that Hawai'i's native biota deserves protection and management. Recent studies demonstrate that native ecosystems will benefit from protective management (Muller-Dombois, Bridges, and Carson 1981).

The Hawaiian biota coevolved with a diverse and rapidly evolving invertebrate fauna. Thus, numerous elements would be expected to be resistant to many of the threats posed by alien invertebrates. As an example, the resistance of Hawaiian cotton to bollworms (Helicoverpa spp.) is being incorporated into some commercial strains of cotton. However, it appears that certain forms of novel alien threats, i.e. those with which segments of the native biota have no previous contact or with which they were not preadapted to cope, may create irreversible changes.

It is clear from this review that social and colonial species of invertebrates--termites, ants, bees, wasps--are by far the most damaging to native species. Disease transmitters are also a serious concern. Generalist species within each trophic level are nearly always more damaging to native communities than are specialists. These attributes can provide a sound predictive basis for assessing potential impacts of new arrivals as well as for establishing guidelines in reviewing proposals for releases for biocontrol or other purposes.

Quarantines

Probably the most cost-effective measure to reduce the negative impacts of alien invertebrates in the Islands is to stiffen quarantine procedures in order to greatly lessen the chance that a harmful alien will be intentionally or inadvertently introduced. Quarantine cannot hope to be absolute in keeping everything out, but it is a method to buy time between crises and allow for the development of management strategies.

In order to be effective, quarantine regulations must be strictly enforced. Public education campaigns must stress the fact that quarantine protects everybody, i.e. the State's economy, the public's health, and the environment. Proper education can make enforcement palatable to travellers. It must, or we have lost. For the harmful aliens we have now are but minor previews of the impacts of a whole host of invertebrates waiting for a ride to our shores. For example, in terms of conspicuousness and extent of negative impacts, Hawai'i so far has fortunately escaped as damaging an alien invertebrate as the gypsy moth in North America (Marshall 1981).

The great isolation of Hawai'i will aid quarantine efforts, for transportation possibilities are limited to long-distance boats and aircraft. These, both military and civilian, must be closely inspected and also treated to prevent the escape of invertebrate stowaways. The immediate areas surrounding ports of entry, such as piers and airports, should be treated to minimize establishment and monitored for incipient infestations, the latter to be dealt with promptly. Shipments of economic commodities and personal goods should be inspected or fumigated as appropriate by qualified personnel.

Nonsensical importations, i.e. importations that have a high risk of harboring pest species and either are non-economical (recreational) or directly compete with a viable local industry, deserve special scrutiny. Some of these appear ludicrous. Dried cow dung, which harbors an unbelievable array of blood-sucking and other arthropod pests, has been imported for cow chip throwing contests. Polo ponies have been air freighted in luxury without quarantine directly between games all over the world (several recent coprophages almost surely arrived by this jet set polo route). Boatloads of untreated Christmas trees arrive every winter with an alarming array of hibernating or diapausing pests. Cut flowers for the lei and florist trade are air-freighted in bulk from other tropical areas, especially the Philippines. Zoo animals, recently especially reptiles, have arrived without quarantine, creating a number of incipient infestations of bloodsucking mites at the zoo and elsewhere in Honolulu (Goff 1980a). Plants and animals are being imported for the home aquarium and pet trade. And finally, plant propagules are shipped in for the botanic gardens and florists, often with their associated fauna still attached. All of these are classed as high risk in regard to the arrival of alien pests, and indeed several recent pests have arrived by each of these routes, including kissing bugs, chiggers, ticks, sepsid dung flies, spiraling whiteflies, plant bugs, and flower-feeding moths. The promoters of high risk importations must recognize that strict measures assuring the absence of alien stowaways must be applied or the activity must be curtailed.

Quarantining living plant importations makes good sense, since great numbers of plant-associated invertebrates have a cryptic stage, either inside or on their host plant. For example, insect eggs are often cryptically attached to the plant and many species actually insert their eggs into plant tissues. These are very difficult or nearly impossible to detect during inspections.

In addition, bulk shipments of certain fresh produce should be regulated to prevent harmful introductions. For example, shipments of watercress, particularly, often harbor an array of potentially detrimental species of snails and slugs (C.C. Christensen, pers. comm.). Since watercress is also produced locally, curtailing its importation would seem to benefit the local economy, as well as reduce the threat of importing pests.

Research Needs

Measures to lessen the impact of alien invertebrates must be based on sound research and firm understanding of ecosystem processes and functioning. Basic to understanding and subsequent management of Hawaiian ecosystems is the need for a more thorough biological survey. Most groups of native insects and other invertebrates are still poorly known taxonomically, even though these groups play a greater role in ecosystem function than they do in analogous continental ecosystems. Management procedures are impossible if the managers cannot recognize or distinguish native from alien species.

Long-term basic ecological studies are required because ecosystem models ideally must be able to distinguish temporary shifts in populations from the more serious irreversible changes in response to new perturbations. Ecosystems are dynamic mosaics of species interacting in complex food webs. Each species is continually adapting and evolving in response to ever-changing biotic and abiotic selective forces.

A number of ecological problems, which require research data before they can be solved, were identified in this review. Among the more critical is the need to monitor the spread and impacts of ants and other highly damaging aliens in Hawaiian ecosystems. More experimental long-term research is especially needed on the autecology of these aliens in order to find their weaknesses, develop environmentally sound but effective controls, and implement mitigative procedures. Studies are needed on the efficacy and environmental impacts of species imported and released for biological control.

Long-term autecological studies are also needed on the rarer or more interesting segments of the native biota, especially invertebrates. Much useful information can come from such studies. For example, Hadfield and Mountain (1981) found that the slow growth rate of the tree snail *Achatinella mustelina* and its low fecundity left it extremely vulnerable to predation pressures. The next step is to find mitigative measures to reduce predation by alien species.

Research data are also needed on the relationships among alien diseases, vectors, reservoirs, and the native biota. Studies on pollination and reproductive strategies of both native and alien flora might provide information leading to the development of management strategies for protecting native species. Additionally, the inclusion of invertebrate surveys and assessment in the environmental impact statement (EIS) process is strongly recommended.

Management

Management recommendations for mitigation of the impacts of alien invertebrates already established center mostly on reducing the novel perturbations that favor populations of the aliens. Our ecological experience is not yet sophisticated enough to propose specific, environmentally sound measures for most problems concerning alien invertebrates. The special constraints of biocontrol will be discussed separately.

A number of alien leaf litter and soil invertebrates are favored by the disturbance caused by feral vertebrates, especially rooting by feral pigs. The relationship among cattle, dung beetles, and mongooses was described above. Reduction of feral vertebrate perturbations will also reduce the impacts of these aliens. Invading alien plants provide food and avenues for the invasion of the forests by alien arthropods. This presents greater opportunities for interactions among these alien invertebrates and native species.

Certain ants and yellowjackets pose severe threats and require special controls in native habitats. In national and state parks, in natural area reserves, and in accessible areas such as along public trails, yellowjacket nests should be searched for and destroyed. Efficient methods of locating nests need to be developed, and their populations should be monitored and further control measures taken wherever their activity increases.

Several of the alien ants are best adapted to exploit disturbed ecosystems, especially continuously cropped agroecosystems (Risch and Carrol 1982; Lubin 1984). This may be related to availability of suitable nesting sites, incomplete ground cover, shorter stature of vegetation, or competition. Removal of disturbances such as grazing by feral ungulates, fire, and forest clearing may minimize or reduce the impacts of these alien predators and slow their spread into forest ecosystems.

The alpine scrub vegetation zone (E2 and E3 in Ripperton and Hosaka 1942), with its low stature plants and abundant rocky substrate, presents an ideal habitat for those ants that can withstand the harsh climate. The possibility that the Argentine ant will establish in Haleakala Crater and do irreparable damage is further enhanced by the presence of large colonies of aphids on alien weeds such as the oenothera aphid Aphis oestlundi on the evening primrose. Research on management of these weeds should begin now before a crisis occurs. In addition, these aphid colonies may provide a handy monitoring station for early detection of the establishment of any of the harmful honeydew-tending ants. The colonies of the Argentine ant near Park headquarters and at Kalahuku should be contained and eradicated if possible. Material, especially that stored on the ground in infested areas (e.g. fencing equipment), should be closely inspected before being carried into Haleakala Crater (Beardsley 1980). An assessment of the status of native invertebrates and plants within the outside areas occupied by the Argentine ant near Park headquarters would provide documentation of the urgency of the problem in this habitat (Beardsley 1980; Fellers and Fellers 1983).

Monitoring the activity of the long-legged ant in lower Kipahulu Valley and research on control is necessary to assure the survival of the native stream fauna there (Hardy 1981), which includes the last known population of the rare and endangered damselfly Megalagrion pacificum.

Biocontrol

The major aegis for purposeful introduction of invertebrates into Hawai'i has been classical biological control (the discovery, importation, and release of an alien species with the expectation that it will control a "pest" population). The method blossomed in Hawai'i in the late 19th and early 20th centuries, largely through the activities of one man, Albert Koebele. There have been some apparent spectacular successes in the control of both weed and animal pests. Records for species introduced are scanty, especially for the early years as Koebele and probably others only recorded those that they felt were successful (Swezey 1931). To date probably over 2,000 invertebrate species have been intentionally imported for biocontrol, but only a part, between 10 and 25%, actually have become established.

Now that the environmental risks of classical biocontrol are recognized, we need to reevalute the methodology and philosophy used by workers in this area (Howarth 1983; Klingman and Coulson 1983; Haas and Pal 1984; Pimentel et al., in press). It must be stressed here, however, that this in no way is meant as criticism of the activities of past or current workers in biocontrol. Biocontrol specialists acted with the best information and rationale available at the time and did what was thought to be in the best interests of human welfare and agricultural and economic development. As with any applied science, biocontrol must change to accommodate the new empirical and theoretical data in order to advance as a discipline. Historically, Hawai'i has been a world leader in developing empirical methodologies and in advancing the theory of biocontrol. It is heartening to note that Hawai'i's agriculturalists are modifying their standard operating procedures in order to address and minimize newly recognized risks.

In a comparison of environmental concerns among pest control procedures, I listed 6 limitations of classical biological control (Howarth 1983). These were that:

1. Classical biocontrol procedures are usually irreversible.
2. The imported organisms may expand their host range and attack non-target organisms.
3. The imported organisms may spread and invade other habitats.
4. The method has been plagued by poor research design on efficacy and environmental impact analyses.
5. Biocontrol needs a better review of cost-benefit analysis.
6. The method requires adequate sophisticated biosystematic and ecological data on both the target species and the control species.

The first priority in control should be understanding the ecology of the pest in relation to the environment and economic loss, with a view of separating aesthetic problems and those with cultural solutions from those with more genuine economic or basic ecological problems. Pest outbreaks fostered by mismanagement of the environment should be solved by instituting proper management procedures, e.g. weedy plant invasion of overgrazed pastures is best corrected by proper range management, such as reducing the number of cattle per acre, instituting a proper rotation schedule, etc.

Improved research on the ecology of both the pest and the proposed control organism will minimize the risks. The ecology of each organism proposed for importation should be worked out in the geographical areas where it already occurs in order to predict its range, habitat preferences, and any special problems before its introduction is attempted. Where classical biocontrol is shown to be the preferable method, it will pay to do the requisite ecological research to find the organism with the best potential for control which presents the least risk to non-target organisms and the environment. Historic introductions for biocontrol indicate that specialist species with narrow host ranges have been better control agents as well as having less impact on non-target organisms than have generalist species.

The current standard operating procedure of testing new importations in quarantine facilities against possible non-target organisms needs to be supported and expanded. Biocontrol agents should in principle not be introduced to control any native species. Considerable extra caution should be exercised on host specificity before any introductions to control species (e.g. Rubus spp.) closely related to native species are considered.

Research and assessment funds should be committed by the proposing agency at the time of introduction to support long-term assessment of the efficacy of the organism against the intended pest and its impacts on non-target organisms. Too many biocontrol "success" stories are based solely on hearsay.

A high priority is to work towards a consensus within the community on what constitutes a pest. We have endured enough of one public agency planting lantana (Lantana camara), melastomas, etc., as ornamentals along roadsides, in parks, and in public places, while another State agency introduces alien herbivores to control them. One State agency has imported alien predators in an attempt to reduce insect damage on haole koa, Leucaena leucocephala, while the national parks and many other land managers spend considerable money in an effort to control this alien weed. In most instances these short-term fixes are detrimental to native species. Let's give the natives a better chance by planning more for long-term solutions.

Conflicts also may arise even among researchers working towards control of pests impacting the native biota. For example, some of the biocontrol agents used against the mosquitoes that vector avian malaria and other diseases among native birds to date have disrupted native aquatic ecosystems and extirpated native species such as the damselfly Megalagrion pacificum. The early indications were that the koa psyllid Psylla uncatoides was a potential threat to both koa and the rare Acacia koaia and would compete with the native fauna associated with those trees; yet the introductions for biocontrol presented risks to some of the native psyllids and perhaps to other small, soft-bodied native foliar arthropods. These potential conflicts over what constitutes a pest and how to effectively deal with it, are best resolved with open review among concerned specialists and the public.

The most effective aegis for this open review is through the preparation of an environmental impact statement for proposed introductions. The history of environmental impacts by alien organisms demonstrates that the EIS process is justified. Persons who introduce animals or plants beyond their natural range undertake a grave responsibility. Society must discourage alien introductions in principle. Proposals for introductions must demonstrate convincingly that the new organisms will not harm the native flora or fauna, human health, or the local economy. Classical biocontrol has been shown to be largely irreversible and to have considerable environmental risks, and therefore should be used only as a last resort for legitimate serious pests. The hit-or-miss, shotgun approach of multiple species introductions espoused by earlier workers must end.

Education

A major factor for mitigating the negative impacts of alien species is education, and many educational recommendations were discussed under each of the above proposed solutions. Many pest problems actually involve only minor aesthetic damage or stem from the public's fear of the perplexing array of strange invertebrates. It is unfortunate that the advertizing and entertainment media prey on and reinforce a general phobia of insects and other "creepy-crawlies." If our educational system could overcome this cultural bias and instill a public appreciation of the aesthetics, right-to-life, interest, and importance of invertebrates in ecosystem functioning and human welfare, we would solve the majority of our "pest" problems.

ACKNOWLEDGEMENTS

I thank my wife, Nancy, for editorial assistance, C.C. Christensen and W.C. Gagne for providing helpful references, and both of them and F.J. Radovsky, C.W. Smith, C.P. Stone, and W.L. Wagner, for reading and commenting on earlier drafts of this manuscript. I also thank R.M. Severns for information on snail conservation.

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