Alien Species and the Extinction Crisis of Hawaii's Invertebrates

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In 1962, Rachel Carson eloquently and convincingly argued that the intensive and widespread use of pesticides was resulting in the pollution of ecosystems, declines in wildlife, and human health problems. These poisons were primarily insecticides used against what she called "an avalanche" of resistant insects. Most people share this concept of insects and other invertebrates as a natural disaster (Kellert 1993), and concerns for invertebrate conservation seem almost oxymoronic. Even the Endangered Species Act withholds protection for any insect viewed as a significant pest. There has never been a documented invertebrate extinction from pesticides (Howarth 1991), but, as is often the case, where our technology fails our bumbling and perseverance succeed. Like mud tracked across a living room floor, as humans perambulate, roll, sail, and fly across the face of the earth, we scatter other organisms into areas they don't belong. For example, over 2500 alien arthropods are now established in Hawaii (Howarth 1990, Howarth et al. 1995, Nishida 1992), with a continuing establishment rate of an appalling 10-20 new species per year (Beardsley 1962, 1979). Unlike chemicals, established alien organisms are permanent, they propagate, and they disperse. The visual result is a homogenization of the biological landscape. The often unseen result is the disappearance of native species, including invertebrates, due to predation, competition and associated diseases of the alien organisms. In this article, I describe how the introduction of alien species into the Hawaiian Islands has resulted in an almost unimaginable decline and extinction of invertebrates, and repercussions on the ecosystems.

Unique Fauna Susceptible to Invasions

Continents typically have large, diverse faunas and comparatively low establishment rates of alien species, therefore ecological consequences of introductions are often small (Simberloff 1995), although there are many significant exceptions (OTA 1993). In contrast, island faunas are characterized by low species richness with the entire absence of certain groups, and many island species have lost competitive or antipredation adaptations (Howarth & Ramsay 1991, Paulay 1994). These features seem to allow alien species to colonize islands more successfully and have major environmental impacts (Carlquist 1965, Simberloff 1995).

In general, more isolated islands have more disharmonic faunas and species with unusual characteristics (Howarth & Ramsay 1991). Hawaii, over 3500 kilometers from any major land mass, is the most isolated island group on earth, and has a correspondingly unusual invertebrate fauna derived from relatively few successful colonists (Simon et al. 1984). For example, only 15% of insect and snail families are represented in Hawaii (Howarth 1990, Solem 1990); one hears no cicadas, sees no lightning bugs, nor originally would have felt the bite of any mosquito, or lost garden plants to slugs. Successful colonizing groups frequently lose characters common in their continental ancestors, and move into ecological niches normally occupied by other groups, thus, Hawaii has flies with no wings, stink bugs with no stink, snails with no shells, and caterpillars that eat flies.

Rather than receiving species from elsewhere, Hawaii's fauna tends to be home grown, with in situ speciation occurring rapidly (Carson 1983) and over very small geographic distances (Otte 1994). It has also allowed spectacular radiations in some lineages, with over 500 species of Drosophila flies and Hyposmocoma moths, and at least 9 other genera that contain over 100 species (Howarth 1990). Hawaii's snail fauna is considered to be the most diverse and unique on earth, with over 1000 endemic species (Solem 1990). With the end of Hawaii's isolation, however, a process of mass extinction began that is rapidly dismantling this archipelago's invertebrate showcase of insular evolution (Zimmerman 1970, Howarth and Ramsay 1991).

Human Impacts on Native Fauna

Human occupation of the Hawaiian islands began with the arrival of the Polynesians about A.D. 400. Largely through agricultural activities, Polynesians extensively altered Hawaii's dry forests, shrublands, and mesic valleys, severely impacting its vegetation, birds, land snails, and probably arthropods (Kirch 1982, Olson & James 1982, Cuddihy & Stone 1990). But Polynesians introduced fewer than 60 plants and animals, and only the Polynesian rat (Rattus exulans) likely had much of an effect on flightless arthropods and land snails. After the arrival of Captain James Cook in 1778, Hawaii's invertebrates continued to suffer from direct habitat loss in low elevations due to humans, and also from the direct and indirect effects of a burgeoning assemblage of alien species. Goats, cattle, horses, sheep, deer, and pigs were introduced in the 1800's and established large feral populations. These animals destroy vegetation by browsing and trampling root systems, and facilitating the dispersal of alien weeds (Stone 1985) such as strawberry guava (Psidium cattleianum), Koster's curse (Clidemia hirta), blackberry (Rubus species), lantana (Lantana camara), and fountain grass (Pennisetum setaceum). These species invade disturbed areas and compete with native species or increase the frequency of fires (Smith 1989, Stone et al. 1992). The impacts of large mammals and alien plants on Hawaiian ecosystems are well documented (Stone & Scott 1985, Cuddihy & Stone 1990) and native invertebrates disappear as their habitats are lost (Foote & Carson 1995).

The best documented decline of a Hawaiian invertebrate is among snails due to the preservation of their shells and their popularity among early naturalists. The genus Carelia was endemic to the island of Kauai and contained Hawaii's largest land snails, some with shells over 85 mm long. The last living specimen was seen in 1950 and all 12 or more species are now believed extinct (Solem 1990). In fact, all the 300+ species of Amastridae, a family of predominately ground dwelling snails endemic to Hawaii, may now be extinct (S. Miller, USFWS, Pacific Islands Office, pers. comm. 1995). This loss of higher level taxa is comparable to other mass extinctions in earth's history (Jablonski 1991) only this one is occurring in a geological blink of an eye.

The extinction of Hawaiian arthropods from alien species-induced habitat loss has undoubtedly been even greater, but most have left no trace of their existence. A mass arthropod extinction that was at least partly documented occurred on the small (ca. 5 km sq.) island of Laysan in the northwestern part of the Hawaiian archipelago. Rabbits were introduced to Laysan about 1903 and were not exterminated until 1923 (Ely & Clapp 1973). In that time, the rabbits almost completely devegetated the island. While much of the vegetation subsequently recovered at least 10 endemic phytophagous insects went extinct. Many Hawaiian arthropods may be more susceptible to extinction than other species because they are more provincial and more ecologically specialized. For example, the extinct weevil, Rhyncogonus bryani was restricted to Laysan and fed exclusively on Chenopodium oahuense. While the plant was decimated, it is now recovering on Laysan and also occurs on numerous other Hawaiian islands. The weevil, however, did not survive the severe reduction of its host plant.

While more difficult to document, the main Hawaiian Islands have also suffered innumerable extinctions of phytophagous insects. Over 100 species of Hawaiian plants are known to be extinct (USFWS 1994) and over 100 more plant extinctions probably went undocumented (L. Mehrhoff, USFWS, Pacific Islands Ecoregion, pers. comm., 1995), along with their compliment of host specific insects. In 1917, a new species of Proterhinus weevil was collected from the last remaining tree of Hibiscadelphus giffardianus on the island of Hawaii. While the tree has been given a reprieve from extinction by propagation of individuals from seed, the weevil, which breeds in senescent branches, was doomed with the death of the last wild tree. Members of the plant bug genus Engytatus typically live on sticky or hairy plants. In Hawaii, three undescribed species are each restricted to a different species of endangered plant. While these plants may recover in the wild, or at least be artificially propagated, it is unlikely that their associated insects will survive such a severe decline in their specialized habitat.

Going Quietly Into That Good Night

Other alien species have a more direct, yet less visible effect on Hawaiian invertebrates (Howarth & Medeiros 1989). Any tropical biologist will tell you that while the lion may be the king of the jungle, the ant is most certainly the queen. Ants and other social insects frequently dominate the ecologies of tropical ecosystems and strongly influence the evolution of certain plants and animals. The Hawaiian invertebrate fauna evolved without the influence of ants or social wasps, and their arrival has been devastating.

Ants can be particularly destructive predators because of their high densities, recruitment behavior, aggressiveness, and broad range of diet (Reimer 1993). These attributes allow some ants to affect prey populations independent of prey density, and ants can therefore locate and destroy isolated populations and individuals (Nafus 1993). At least 36 species of ants are known to be established in the Hawaiian Islands, and particularly aggressive species have had severe effects on the native insect fauna (Zimmerman 1948). By the late 1870's, the big-headed ant (Pheidole megacephala) was present in Hawaii and its predation on native insects was noted by the early Hawaiian naturalist R.C.L. Perkins (1913) "It may be said that no native Hawaiian Coleoptera insect can resist this predator, and it is practically useless to attempt to collect where it is well established. Just on the limits of its range one may occasionally meet with a few native beetles, e.g.Qspecies of Plagithmysus, often with these ants attached to their legs and bodies, but sooner or later they are quite exterminated from these localities." With few exceptions, native insects have been eliminated from areas where the big-headed ant is present (Perkins 1913, Gagne 1979, Gillespie & Reimer 1993), and it has been documented to completely exterminate populations of native insects. It has also been implicated in the extinction of the endodontid land snail fauna in Hawaii and on other Pacific islands (Solem 1990).

The Argentine ant (Iridomyrmex humilis) was discovered on the island of Oahu in 1940 and is now established on all the main islands. Unlike the big-headed ant, the Argentine ant is primarily confined to higher elevations (Reimer et al. 1990). This species has been demonstrated to reduce populations or even eliminate native arthropods at high elevations in Haleakala National Park on Maui (Cole et al. 1992). While this species does not disperse by flight, colonies are moved about with soil and construction material, and a colony was recently discovered on an isolated peak on the island of Oahu under a radio tower. Numerous other ant species are recognized as threats to native invertebrates (Figure 3), and additional species become established yearly, including one new ant which was discovered in Hawaii while this article was being written (N. Reimer, Hawaii Dept. of Agriculture, pers. comm., 1995).

Another group of social insects that are voracious predators and were originally absent from Hawaii are yellowjacket wasps (Hymenoptera: Vespidae). In 1977, an aggressive race of the western yellowjacket (Paravespula pennsylvanica) became established in Hawaii and is now abundant at most higher elevations (Gambino et al. 1990). In Haleakala National Park on Maui, yellowjackets were found to forage predominantly on native arthropods (Gambino et al. 1987, Gambino & Loope 1992). Overwintering yellowjacket colonies in Hawaii can produce over half a million foragers that consume tens of millions of arthropods, and there is evidence for localized reduction in native arthropod abundance (Gambino & Loope 1992). The establishment of this species on the island of Hawaii corresponded with a significant decline in some species of endemic Drosophila flies (Carson 1986). Hawaii has only a handful of freshwater fishes, and all but one are predominantly herbivorous. The aquatic stages of Hawaii's endemic Megalagrion damselflies, therefore, evolved largely in the absence of fish predation. Particularly on the populous island of Oahu, native damselflies which could be found in the city of Honolulu only 10 years ago have now virtually disappeared. Most populations now occur only in remote stream drainages or at high elevations. This decline in native damselflies was associated with a proliferation of the aquarium fish trade in Hawaii (Devick 1991), because fish hobbyists sometimes release these pets into the wild where they become established. Freshwater aquatic habitats on Oahu are now choked with 45 varieties of alien fish, from guppies and swordtails to armored catfish, needlefish and even piranha (Devick 1991). Hawaii's damselflies have succumbed to this onslaught and six species are now candidates for Federal listing.

I Know an Old Lady who Swallowed a Spider

Classical biological control involves the purposeful release of a predator or parasite into a novel area to control a pest species. Hawaii has long been active in classical biological control, and between 1890 and 1985, 243 alien species were introduced, sometimes with the specific intent of reducing populations of native Hawaiian organisms (Funasaki et al. 1988, Lai 1988). The endangered Oahu tree snails in the genus Achatinella (Figure 5) were experiencing declines and extinctions due to habitat loss and overcollecting since the arrival of the Polynesians (Hadfield 1986), but the coup de grace was delivered from a biological control agent. In 1956, the predatory snail, Euglandina rosea, was introduced from Florida to Hawaii as a biological control agent for the giant African snail, Achatina fulica. While it has not been demonstrated to control the target pest, it has been documented to completely exterminate populations of endangered Achatinella (Hadfield et al. 1993). This predator is slowly reaching the last, isolated populations of Achatinella high in the Koolau Moutains of Oahu, and is now even foraging in streams, threatening Hawaii's endemic freshwater snails (Kinsey 1992).

Hawaii's insects have also suffered extensively from biological control. For example, the Koa bug (Coleotichus blackburniae) is Hawaii's largest and most spectacular native true bug. Historically, the koa bug was known from all the major Hawaiian islands and was easy to observe because hundreds of individuals could sometimes be seen on a single tree. Until the 1960's, the Koa bug was a very common insect and could frequently be found on koa trees within the city of Honolulu. In 1962, several parasites were released in Hawaii to control a pest stink bug (Nezara viridula), despite the fact that laboratory tests demonstrated that they would also attack the native koa bug (Davis 1964). Subsequent field observations confirmed that some of these parasites were attacking koa bugs in the wild (Howarth 1983). The koa bug is now extremely rare (Howarth et al. 1995) and the spectacular aggregations of this insect may never be enjoyed by future generations.

Hawaii's forest are also polluted with parasites introduced for control of pest Lepidoptera (Howarth et al. 1995). The effects of these parasites may not be limited to direct impacts on the native Lepidoptera fauna (Gagne & Howarth 1985), but may have also contributed to the degradation of an entire ecosystem. Prior to the purposeful introduction of these parasites, almost every year the koa forests on at least Hawaii and Maui islands experienced partial defoliation from the native koa moth caterpillars (Scotorythra paludicola) (R.C.L. Perkins, in Swezey 1926). During these periods the caterpillars were an important food source for birds, as observed by Perkins (1913) "Native birds attracted in thousands by the abundance of this [caterpillars], one of their favorite foods, were gorged to repletion, and the starving caterpillars formed in writhing masses on the ground beneath the tall koa trees. The dropping of excrement from the trees on the dead leaves made a rattling noise as of a hailstorm." Protein provided by insect prey can be the limiting factor in the breeding success of birds (Martin 1987, Boutin 1990), and Rodenhouse and Holmes (1992) demonstrated a reduction in the reproductive success of warblers resulting from a decline in the caterpillar prey base. Now only rarely (1926, 1953, 1977, and 1982) do Hawaiian koa forests experience any defoliation because the koa moth is under "complete biological control" from alien parasites (Lai 1988). The increased parasite pressure on this species has apparently restricted these normal, seasonal population increases. The elimination of this important food source may be a contributing factor to the decline of Hawaii's forest birds (Banko 1978, Gagne 1981), and the ecological functions they served as pollinators and seed dispersers (Carlquist 1980, Cox 1983, Lammers & Freeman 1986).

Saving The Little Things that Run the World

Even when convinced of the mass extinctions occurring among Hawaii's invertebrates, resource managers frequently point out that limited conservation resources need to be allocated to higher priority species. But it is ecologically indefensible and shortsighted to attempt to manage for the conservation and recovery of species without considering the other organisms which constitute the biological components of the ecosystem (USFWS 1994). For example, both species in the endemic Hawaiian plant genus Brighamia are listed as endangered. While these taxa are easily propagated, wild plants must be hand pollinated because the natural pollinator, a moth, is extinct. Thus, we can win battles by fencing a natural area, pulling weeds, and shooting pigs, but unless the conservation needs of all the organisms are addressed, we will still lose the war for the forest. Invertebrates are the glue that hold HawaiiUs ecosystems together.

What can we do? First we must recognize that management of natural areas and ecosystems will require inclusion of organisms in addition to plants and birds. We need to develop sophisticated chemical and pheromone controls for predatory snails, yellowjacket wasps and other alien invertebrate species. We must cooperate with the appropriate Federal and State agencies to slow or stop the influx of additional alien species. Finally, we must recognize that the purposeful introduction of alien organisms is one of our most powerful technologies, and mistakes are irreversible and sometimes devastating (Howarth 1983, 1991). Present Federal laws regulating the release of invertebrate biocontrol agents are ambiguous and insufficient (Miller & Aplet 1993). The State of Hawaii review process presently excludes most Federal and private agencies charged with management of natural resources in Hawaii. In 1995, Hawaii's silent spring is occurring not because increasing chemical usage can't kill invertebrates, but because poorly regulated transportation and biological technologies can.

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Literature Cited

Banko, W.E. 1978. "Some limiting factors and research needs of endangered Hawaiian forest birds." In C.W. Smith, editor, Proceedings, 2nd Conference on Natural Science. Hawaii Volcanoes National Park. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu.

Beardsley, J.W. 1962. On accidental immigration and establishment of terrestrial arthropods in Hawaii during recent years. Proceedings of the Hawaiian Entomological Society 18: 99-109.

Beardsley, J.W. 1979. New immigrant insects in Hawaii: 1962 through 1976. Proceedings of the Hawaiian Entomological Society 23: 35-44.

Boutin, S. 1990. Food supplementation experiments with vertebrates: patterns, problems, and the future. Canadian Journal of Zoology 68: 203-220.

Carlquist, S. 1965. Island life. Natural History Press, Garden City, New York.

Carlquist, S. 1980. Hawaii: A Natural History. Second Edition. SB Printers, Inc., Honolulu, Hawaii.

Carson, H.L. 1983. Chromosomal sequences and interisland colonization in Hawaiian Drosophila. Genetics 103: 465-482.

Carson, H.L. 1986. "Drosophila populations in the OloaUa tract, Hawaii Volcanoes National Park, 1971-1986." In Proceedings of the 6th Conference on Natural. Science, Hawaii Volcanoes National Park. June 10-13, 1986. Cooperative National Park Resources Studies Unit, Hawaii.

Carson, R L. 1962. Silent Spring. Houghton Mifflin Company, New York.

Cole, F.R., A.C. Medeiros, L.L. Loope and W.W. Zuehlke. 1992. Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. Ecology 73:1313-1322.

Cox, P.A. 1983. Extinction of the Hawaiian avifauna resulted in a change of pollinators for the ieie, Freycinetia arborea. Oikos 41: 195-199.

Cuddihy, L.W. and C.P. Stone. 1990. Alteration of Native Hawaiian Vegetation; Effects of Humans, Their Activities and Introductions. Cooperative National Park Resources Studies Unit, Honolulu, Hawaii.

Davis, C.J. 1964. The introduction, propagation, liberation, and establishment of parasites to control Nezara viridula variety smargdula (Fabricius) in Hawaii (Heteroptera: Pentatomidae). Proceedings of the Hawaiian

Entomological Society 28:369-375.

Devick, W.S. 1991. "Patterns of introduction of aquatic organisms to Hawaiian freshwater habitats" In W.S. Devick, editor, New Directions in Research, Management and Conservation of Hawaiian Freshwater Stream Ecosystems, Proceedings of the 1990 Symposium on Freshwater Stream Biology and Fisheries Management, Department of Land and Natural Resources, Honolulu, Hawaii.

Ely, C.A. and R.B. Clapp. 1973. The natural history of Laysan island, Northwestern Hawaiian Islands. Atoll Research Bulletin 171:1-361.

Foote, D. and H.L. Carson. 1995. "Drosophila as monitors of change in Hawaiian ecosystems." In E.T. LaRoe, G.S. Farris, C.E. Puckett, P.D. Doran, and M.J. Mac, editors, Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems. U.S. Department of Interior, National Biological Service, Washington D.C.

Funasaki, G.Y., P. L. Lai, L.M. Nakahara, J.W. Beardsley and A.K. Ota. 1988. A review of biological control introductions in Hawaii: 1890 to 1985. Proceedings of the Hawaiian Entomological Society 28:105-160.

Gagne, W.C. 1979. Canopy-associated arthropods in Acacia koa and Metrosideros tree communities along an altitudinal transect on Hawaii Island. Pacific Insects 21:56-82.

Gagne, W.C. 1981. "Altitudinal distribution and composition of arthropods in ohi'a (Metrosideros collina ssp. polymorpha) canopies in Hawaii Volcanoes National Park with ecological implications for some native biota." In Proceedings, 3rd Conference on Natural Science, Hawaii Volcanoes National Park.

Gagne, W.C. and F.G. Howarth. 1985. "Conservation status of endemic Hawaiian Lepidoptera" In Proceedings of the 3rd Congress of European Lepidopterologists. Cambridge 1982. Societus Europaea Lepidopterologica, Karluhe.

Gambino, P., A.C. Medeiros, and L.L. Loope. 1987. Introduced vespids Paravespula pennsylvanica prey on MauiUs endemic arthropod fauna. Journal of Tropical Ecology 3:169-170.

Gambino, P., A.C. Medeiros, and L.L. Loope. 1990. Invasion and colonization of upper elevations on East Maui (Hawaii) by Paravespula pennsylvanica (Hymenoptera: Vespidae). Annals of the Entomological Society of America 83:1088-1095.

Gambino, P. and L.L. Loope. 1992. Yellowjacket Vespula pennsylvanica biology and abatement in the National Parks of Hawaii. Cooperative National Park Resources Studies Unit, Hawaii, Technical Report 86:1-41.

Gillespie, R.G. and N. Reimer. 1993. The effect of alien predatory ants (Hymenoptera: Formicidae) on Hawaiian endemic spiders (Araneae: Tetragnathidae). Pacific Science 47:21-33.

Hadfield, M.G. 1986. Extinction in Hawaiian achatinelline snails. Malacologia 27:67-81.

Hadfield, M.G., S.E. Miller, and A.H. Carwile. 1993. The decimation of endemic Hawai'ian tree snails by alien predators. American Zoologist 33:610-622.

Howarth, F.G. 1983. Biological control: panacea or Pandora's box? Proceedings of the Hawaiian Entomological. Society 24:239-244.

Howarth, F.G. 1990. Hawaiian terrestrial arthropods: An overview. Bishop Museum Occasional Papers 30:4-26.

Howarth, F.G. 1991. Environmental impacts of classical biological control. Annual Review of Entomology 36:485-509.

Howarth, F.G., G. Nishida, and A. Asquith. 1995. Insects of Hawaii: Status and Trends. In E.T. LaRoe, G.S. Farris, C.E. Puckett, P.D. Doran, and M.J. Mac, editors, Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems. U.S. Department of Interior, National Biological Service, Washington D.C.

Howarth, F.G. and A.C. Medeiros. 1989. "Non-native invertebrates." In C.P. Stone and D.B. Stone, editors, Conservation Biology in Hawaii. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, Hawaii.

Howarth, F.G. and G.W. Ramsay. 1991. "The conservation of island insects and their habitats.". In N.M Collins and J.A. Thomas, editors, The Conservation of Insects and Their Habitats, Academic Press, London.

Jablonski, D. 1991. Extinctions: A paleontological perspective. Science 253:754-757.

Kellert, S.R. 1993. Values and Perceptions of Invertebrates. Conservation Biology 7:845-855.

Kinzie III, R.A. 1992. Predation by the introduced carnivorous snail Euglandina rosea (Ferussac) on endemic aquatic lymnaeid snails in Hawai'i. Biological Conservation 60:149-155.

Kirch, P.V. 1982. The impact of the prehistoric polynesians on the Hawaiian ecosystem. Pacific Science 36:1-14.

Lai, P. Y. 1988. Biological control: A positive point of view. Proceedings of the Hawaiian Entomological Society 28:179-190.

Lammers, T.G. and C.E. Freeman. 1986. Ornithophily among the Hawaiian Lobelioideae (Campanulaceae): Evidence from floral nectar sugar compositions. American Journal of Botany 73:1613-1619.

Martin, T.E. 1987. Food as a limit on breeding birds: a life-history perspective. Annual Review of Ecology and Systematics 18:453-487.

Miller, M. and G. Aplet. 1993. Biological control: A little knowledge is a dangerous thing. Rutgers Law Review 45:285-334.

Nafus, D.M. 1993. Biological control agents and native parasites in the population system of the butterfly Hypolimnas bolinas (L.) (Lepidoptera: Nymphalidae). Micronesica, Suppl. 4:17-23.

Nishida, G.M., Ed. 1992. Hawaiian Terrestrial Arthropod Checklist. Bishop Museum Technical Report No. [1]. 262 pp.

Office of Technological Assessment. 1993. Harmful Non-Indigenous Species in the United States, OTA-F-565, Washington, D.C.

Olson, S.L. and H.F. James. 1982. Prodromus of the fossil avifauna of the Hawaiian Islands. Smithsonian Contributions in Zoology 365:1-59.

Otte, D. 1994. The Crickets of Hawaii: Origin, Systematics and Evolution. The Orthopterists Society, Philadelphia, Pennsylvania.

Paulay, G. 1994. Biodiversity on oceanic islands: Its origin and extinction. American Zoologist 34:134-144.

Perkins, R.C.L. 1913. "Introduction." In D. Sharp, editor, Fauna Hawaiiensis. Cambridge University Press, Cambridge.

Reimer, N.J. 1993. "Distribution and impact of alien ants in vulnerable Hawaiian ecosystems." In D.F. Williams, editor, Exotic Ants: Biology, Impact, and Control of Introduced Species. Westview Press, Boulder, Colorado.

Reimer, N., J.W. Beardsley and G. Jahn. 1990. "Pest ants in Hawaii." In R.K.Vander Meer, K. Jaffe and A. Cedeno, editors, Applied Myrmecology: A World Perspective. Westview Press, Boulder, Colorado.

Rodenhouse, N.L. and R.T. Holmes. 1992. Results of experimental and natural food reductions for breeding black-throated warblers. Ecology 73:357-372.

Simberloff, D. 1995. Why do introduced species appear to devastate islands mare than mainland areas? Pacific Science 49:87-97.

Simon, C.M., W.C. Gagne, F.C. Howarth, and F.J. Radovsky. 1984. Hawaii: A natural entomological laboratory. Bulletin of the Entomological Society of America 30:8-17.

Smith, C.W. 1989. "Non-native plants." In C.P. Stone, and D.B. Stone, editors, Conservation Biology in Hawaii. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, Hawaii.

Solem, A. 1990. How many Hawaiian land snail species are left? and what we can do for them. Bishop Museum Occasional Papers 30:27-40.

Stone, C.P. 1985. "Alien animals in Hawaii's native ecosystems: toward controlling the adverse effects of introduced vertebrates." In C.P. Stone, and J.M. Scott, editors, Hawaii's Terrestrial Ecosystems: Preservation and Management. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, Hawaii.

Stone, C.P. and J.M. Scott. 1985. Hawai'i's Terrestrial Ecosystems: Preservation and Management. Cooperative National Park Resources Studies Unit, University of Hawaii, Honolulu.

Stone, C.P., C.W. Smith and J.T. Tunison. 1992. Alien plant invasions in native ecosystems of Hawaii: Management and Research. University of Hawaii Press, Honolulu, Hawaii.

Swezey, O.H. 1926. Reports on defoliation of Maui Koa forests by caterpillars. Hawaiian Planters' Record 30:354-362.

U.S. Fish and Wildlife Service. 1994. Draft Ecoregion Plan for the Pacific Islands Office. U.S. Fish and Wildlife Service, Honolulu, Hawaii..

Zimmerman, E.C. 1948. Insects of Hawaii. Vol. 1. Introduction. University of Hawaii Press, Honolulu.

Zimmerman, E.C. 1970. Adaptive radiation in Hawaii with special reference to insects. Biotropica 2:32-38.
