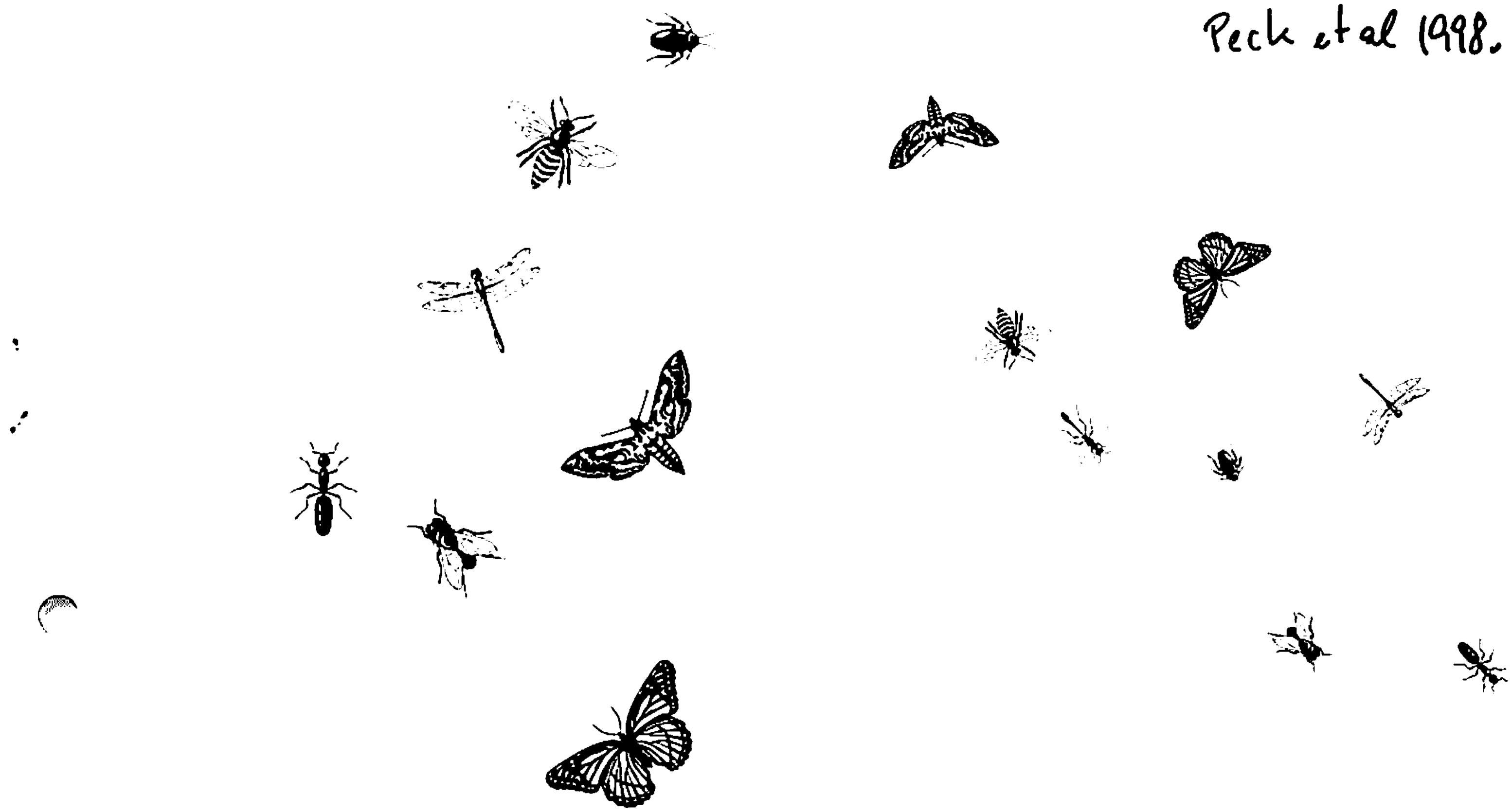
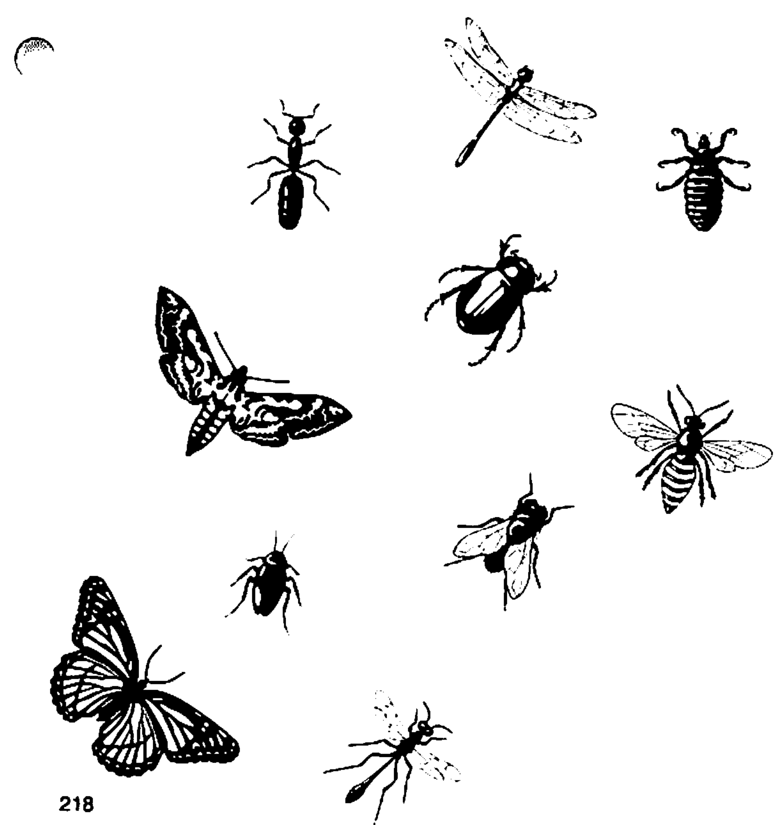
Peck et al 1998.



Introduced Insect Fauna of an Oceanic Archipelago: The Galápagos Islands, Ecuador



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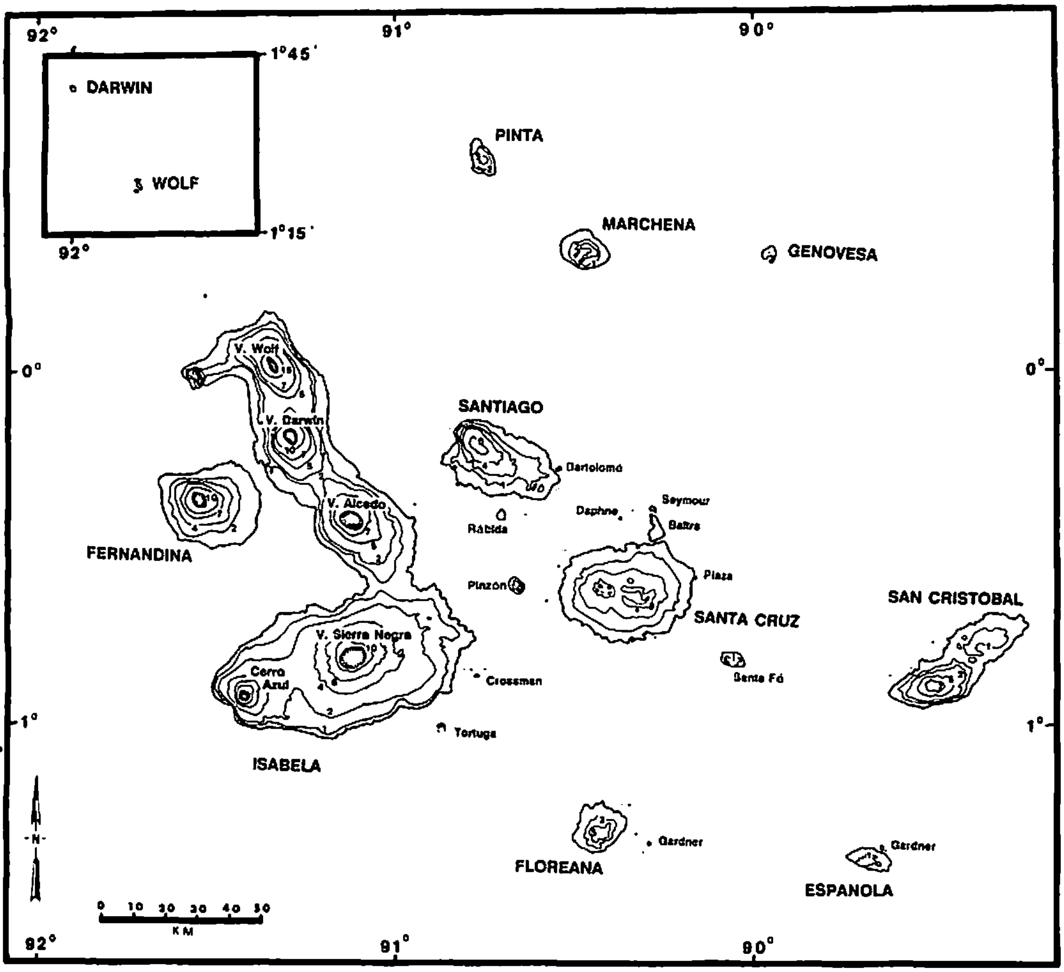

Fig.1. Positions of the Islands of the Galápagos Archipelago, Ecuador. Numbers indicate contour intervals in hundreds of meters. Note the five principal volcanos (including Cerro Azul) that have united to form Isabela Island.

Oceanic islands are susceptible to invasion by exotic species of plants and animals that are introduced either intentionally or unintentionally by human action. Most tropical oceanic islands now have insect faunas that have changed markedly since their discovery by humans. The changes occurred with the introduction of foreign species by aboriginal peoples and later by colonization activities of Europeans (Carlquist 1965, 1974). For instance, the Hawaiian Islands now have more than 3,200 alien species of arthropods (Howarth 1990) and 2,621 species of introduced insects. Approximately 500 of these insects can be classed as pests (Beardsley 1991). More than 416 insect species were introduced intentionally (Nishida 1994), and it now is difficult to find indigenous insect species in most lowland areas of the Hawaiian islands. The faunal change in almost all tropical island

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insect faunas occurred before scientific inventories could document the processes and stages of change.

The Galápagos Islands of Ecuador are the world's most pristine, best preserved and protected, tropical oceanic island ecosystem. More than 95% of the land area of the Islands now is protected in the Galápagos National Park.The islands have been well studied and were little altered until the late 19th and early 20th centuries. The unique biota of the Galápagos Archipelago developed in almost complete isolation during some 3.5 million years. Natural colonization events from the continental mainland were infrequent; in insects, these now are estimated to be about one every 2,000 years (Peck 1996a). With the European discovery of the islands by Bishop Tomas de Berlanga of Panama in 1535, human contact began a process of introduction of additional species of plants and animals. These introductions often had disastrous consequences on the naturally occurring species and upon community structure.

The introduction of exotic biotas to the Galápagos was the result of many causes, but most were either intentionally or accidentally associated with horticulture, agriculture, and livestock. Some introductions undoubtedly occurred in the first 300 years after European discovery, during short visits by pirate and whaling vessels. Many introductions can be attributed to the first period of permanent human colonization from the 1830s to 1890s, which mostly was concentrated on the islands of San Cristobal and Floreana. Additional introductions probably date from the 1920s to the 1970s and accompanied the waves of agriculturally motivated settlers moving to the Galápagos at that time, especially to Isabela and Santa Cruz islands (Hickman 1985), and the importation of wartime materiel and supplies in World War II. A boom in the eco-tourism industry has caused a massive influx of rural and urban settlers from mainland Ecuador in the past two decades. As a consequence, more than 500 nonindigenous species of plants now have become established, and various birds and lizards as well as livestock have been imported and become feral (McFarland and Cifuentes 1996).

Baert (1994) discussed the accidental introduction of various invertebrates and some of the problems that these have caused. Approximately one half of the spiders known from the Archipelago seem to be introduced species (Baert 1994). The milliped *Asiomorpha coarctata* (Sausseur), a large black species with yellow paranota, now is abundant as a detritivore in pastures in the agriculture zone on Santa Cruz. The cosmopolitan terrestrial isopods *Porcelio laevis* Latreille, *P. scaber* Latreille, and *Porcellionides pruinosus* (Brandt), all of Mediterranean origin, were present by 1964 and now are abundant detritivores in arid-zone forest leaf litter on many of the islands. Endemic terrestrial isopods now can be found only on the small outlying islands not inhabited by the cosmopolitan species. Introduced earthworms are frequent in agricultural areas of the islands. Even unlikely invertebrate introductions, such as terrestrial flatworms and onychophorans, have been found in disturbed areas on Santa Cruz Island (S.B.P. unpublished data).

For several years, our research team has been constructing a species inventory and ecological-evolutionary analysis of the entire insect fauna of the Galápagos Islands. As a part of this project, we have been interested in identifying the modes by which insect colonists probably reached the Galápagos (Peck 1994a, 1996a). We evaluated the identity, ecology, and distribution of each of these insect species and proposed a hypothesis for each species being endemic, native, or introduced. It is useful for several reasons to now make available this list of species of insects that probably were introduced, a summary of the most probable way they were introduced, and a list of the islands on which they now occur. It is of both academic and applied interest to understand the diversity, mode of introduction, and spread of this part of the insect fauna and to help plan strategies for protection and preservation of the unique Galápagos ecosystem. This study documents an accidentally introduced tropical island insect fauna more fully than any previous study outside of Hawaii.

Materials and Methods

Extensive earlier entomological literature on Galápagos insects, combined with the results of the field work of others in the past 30 years and our work in the past 10 years, allows us to itemize the composition, origin, and development of the fauna of introduced insects in the Galápagos Archipelago. Our sampling program was 15 months of field work between 1985 and 1996. We sampled all major islands (Fig. 1) and all elevational-climatic life zones by standard insect collecting techniques (Fig. 2). These included hand searching under rocks and logs and in litter; searching, beating, and sweeping vegetation during nighttime and

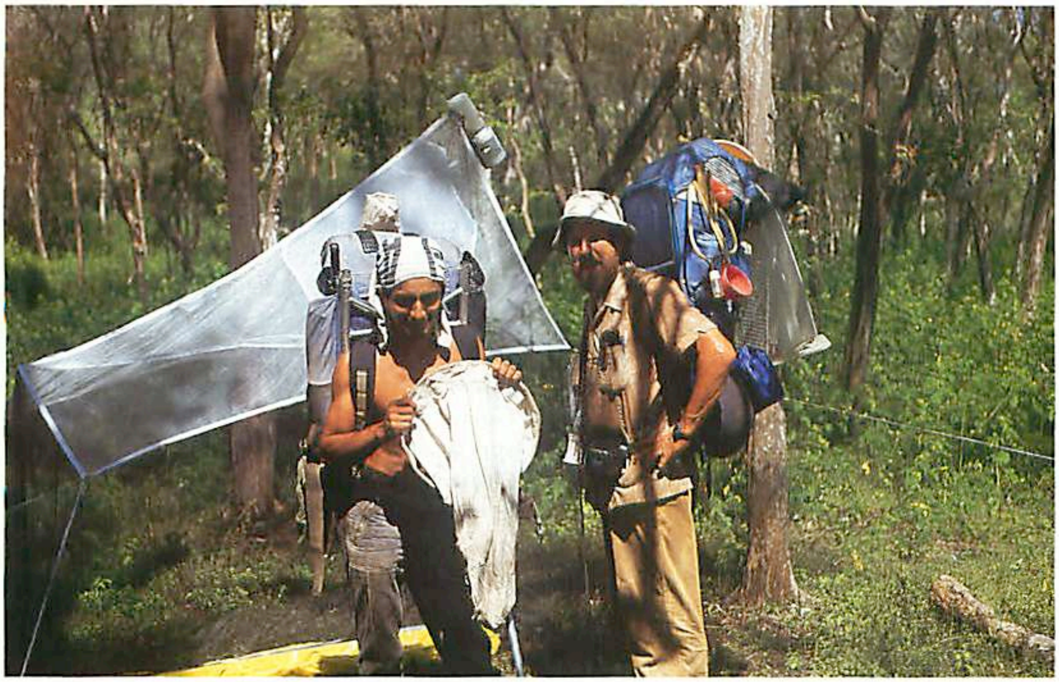

Fig.2. Insect sampling on the large uninhabited islands requires that all equipment be backpacked into interior collecting stations. This transition zone forest on Santiago Island has a qualitatively lowered insect diversity because of large numbers of the introduced little red fire ant.

daytime; using baited and unbaited pitfall traps, Malaise, yellow pan traps, and flight-intercept traps (FIT); collecting at night at ultraviolet and white lights; net collecting of day-active specimens; and collecting in special habitats and by special methods such as along "oatmeal trails" at night, in caves, in bird nests, and Berlese extraction of leaf litter and soil (Fig. 3). The emphasis of our sampling was in undisturbed habitats, but villages and farms also were sampled. More than 50,000 insect specimens have been identified or sorted to species level. Additional new material has been examined from collections of the Bernice P. Bishop Museum (Honolulu), California Academy of Sciences (San Francisco), Museum of Comparative Zoology (Cambridge), Belgian Royal Institute of Natural Sciences (Brussels), and the Charles Darwin Research Station (Puerto Ayora, Isla Santa Cruz). In addition to recording distributional, habitat, seasonal, and other bionomic data for each species, we categorized these species as endemic (not naturally occurring outside of the archipelago), native (probably naturally occurring in both the Galápagos and elsewhere in the New World tropics, especially Central America and northwestern South America), and introduced (probably occurring in the Galápagos because of accidental transport by human agency).

Currently, at least 712 probably endemic species, 818 probably native species, and 292 probably introduced species have been recognized. Voucher specimens are in our collections. It has been possible to assign species names to roughly 90% of these. The exception is the Hymenoptera where the proportion of named species is very low (approximately 30%). This study focuses only on the named species. The actual details and numbers presented here will eventually change as additional species are identified, but the generalizations will not change significantly.

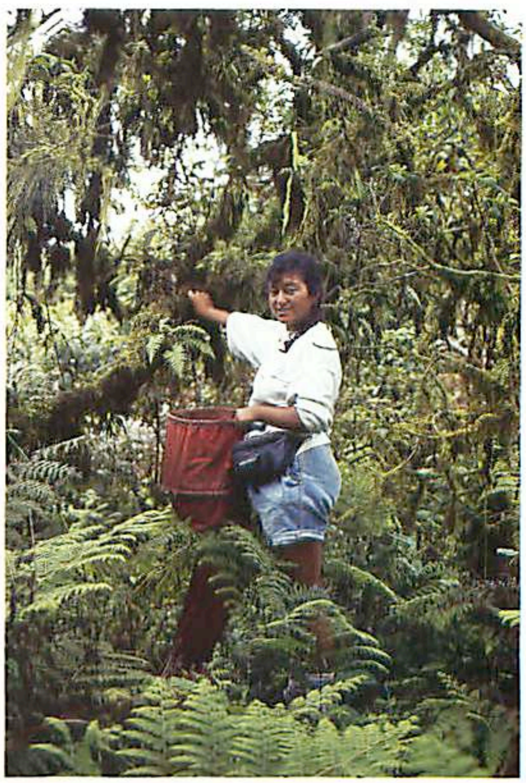

Fig.3. Few people are aware of the humid cloud forest patches on some of the higher islands of the Galápagos. These habitats have been penetrated the least by introduced insects.

There is a growing tendency in the literature of economic entomology to favor the use of the terms "adventive" or "immigrant" as categories for insects that originated elsewhere and were not introduced deliberately to the area under discussion (Frank and McCoy 1990). To adopt these words now for the Galápagos serves no useful purpose. We continue to use the term "introduced" to mean species that were brought by humans to the Galápagos, in the same sense in which it has been used for all previous literature on Galápagos biotas. Although humans intentionally have brought many domestic and some wild animals and both cultivated and weedy plants to the Galápagos, we know of no examples of the intentional introduction of arthropods (even the honeybee, *Apis mellifera* L.). BIOCAT, the worldwide database of biological control introductions of the International Institute of Biological Control (of CABI, London, UK) has no records of intentional Galápagos introductions. The policy of the Galápagos National Park has been to forbid intentional introductions, even for biocontrol purposes.

We list probable introduced insect species in Table 1. This list is a combination of information from an extensive scientific literature, new data gained from study of the museum collections mentioned above, and our field work. Literature documentation of insect collecting expeditions and specimen records before 1977 can be found in Linsley and Usinger (1966) and Linsley (1977). Records from 1985, 1989, 1990, 1991, and 1996 are from our field work, and some have been published previously (e.g., Peck 1996a, b; Peck and Roth 1992). The literature documenting all these species is too extensive to present here. We will cite it in full elsewhere.

Proving that a species has been introduced accidentally usually is not completely possible. Rather, we made deductions from what is known about the species and decided whether or not it more likely arrived in the islands on its own and by natural means, or with human help. The four clues that a species probably has been introduced are as follows: (1) it usually occurs in association with cultivated or introduced plants and livestock; (2) it lives in association with buildings and agricultural or stored products; (3) its first appearance or main habitat was in altered or disturbed areas of farms or cultivated fields or in villages; and (4) it generally is cosmopolitan or tropicopolitan in distribution, suspected of being introduced to other parts of the world by human activity, and frequently called a "tramp" species.

There are some problematical cases. The potential margin of error is highest for Hymenoptera, where 253 species are known but only 77 can now be identified to species; 31 of these 77 species are judged to be introductions. For some parasitoid Hymenoptera, the primary occurrence of a named species in a country other than continental Ecuador was interpreted as evidence of accidental human introduction, although aerial dispersal cannot be discounted. For example, *Trissolcus teretis* Johnson (Scelionidae) is known only from the Galápagos and Florida. It could be more widespread across South America but that is unknown. Hymenopteran parasitoids known from continental South America (e.g., *Cheiloneurus elegans elegantissimus* DeSantis from Brazil and the Galápagos) may be assumed to have a high probability of being introduced by human transport in or on their hosts (mealybugs and others). Some parasitoids (e.g., *Encarsia pergandiella* Howard and *Venturia canescens* Gravenhorst) are ubiquitous and may have arrived by either human transport or wind. Because they most frequently are associated with humans, we assumed human transport. When suspect species such as the psocid *Liposcelis entomophilus* Enderlein (Liposcelidae) and the scale insect *Orthezia praelonga* Douglas (Ortheziidae) are known only from outlying and little disturbed islands, such as Pinta, Genovesa, or Fernandina, we conservatively considered them to be natural dispersals and have not listed them here.

We also estimated the most probable mode of introduction for each species. This was derived from knowing where adults and immatures of the species live and from the species hosts, associations, habitats, and habits. We also listed the year of the first collection record of the species and the islands upon which each species now is known to occur. Islands were not indicated individually if the species was known from eight or more main islands because species that are this widespread are not helpful in identifying the foci of introduction from which the species spread.

Results

There now are at least 292 probable examples of unintentional introductions of insect species to the Galápagos (Table 1). These are in 16 insect orders (Table 2). Because our sampling did not focus on agricultural or urban areas (Fig. 4), there still may be other species present that we did not find or have not as yet *(continued on page 230)*

Table 1. Insect species known from the Galápagos that were probably or certainly introduced

Scientific name and Common name[a]	Probable mode of introduction of the species[b]	First record[c]	Known on Island
Diplura (bristle-tails)			
Japygidae			
Parajapyx isabellae (Grassi)	In soil	1964	SCz
Thysanura (silverfish)			
Nicoletiidae			
Nicoletia meinerti Silvestri	In soil	1964	Isa, SCz
Orthoptera (katydids and crickets)			
Tettigoniidae			
Copiphora brevicauda Karny	On ships (or plants)	1989	Isa, SCl, SCz
Gryllidae			
Anaxipha (*peruviana* Saussure?)	On ships (or plants)	1970	Flo, Isa, SCl, SCz, Sgo
Gryllodes sigillatus (Walker), decorated cricket	On ships (or plants)	1989	Gen, SCz, SCl
Hygronemobius sp.	In plant debris?	1996	SCz
Blattodea (cockroaches)			
Blattidae			
Periplaneta americana (L.), American cockroach	In goods on ships	1877	Flo, Gen, Isa, SCl, SCz
P. australasiae (F.), Australian cockroach	In goods on ships	1889	Flo, Isa, SCl, SCz
P. brunnea Burmeister, brown cockroach	In goods on ships	1920	SCl
Blattellidae			
Anaplecta lateralis (Burmeister)	In goods on ships	1991	SCz
Blattella germanica (L.), German cockroach	In goods on ships	1920	Esp, SCz
Symploce pallens (Stephens)	In goods on ships	1916	On 12 islands
Blaberidae			
Blaberus parabolicus Walker	In goods on ships	1989	SCl, SCz
Nauphoeta cinerea (Olivier), cinereous cockroach	In goods on ships	1893	Flo, SCl
Phoetalia pallida (Brunner)	In goods on ships	1920	SCl
Pycnoscelis surinamensis (L.), Surinam cockroach	In goods on ships	1877	On 9 islands
Rhyparobia maderae (F.), Madeira cockroach	In goods on ships	1989	SCl
Dermaptera (earwigs)			
Carcinophoridae			
Euborellia annulipes (Lucas), ringlegged earwig	In soil	1901	Flo, Isa, SCl, SCz, Sgo
Labiidae			
Circolabia arcuata (Scudder)	In soil	1964	Flo, SCl, SCz
Labia annulata (F.)	In soil	1991	SCl
Labia curvicauda (Motschoulsky)	In soil	1991	SCz
Embiidina (web-spinners)			
Oligotomidae			
Oligotoma saundersii (Westwood)	On plants	1991	SCz
Psocoptera (bark lice)			
Lepidopsocidae			
Echmepteryx madagascariensis Kolbe	On plants	1967	Flo, Isa, SCz
Psoquillidae			
Psoquilla marginepunctata Hagen	Stored products	1967	SCz
Liposcelidae			
Embidopsocus pauliani Badonnel	Stored products	1967	SCl
Caeciliidae			
Caecilius insularum Mockford	On plants	1967	Isa, SCz, Sgo
Lachesillidae			
Lachesilla aethiopica Enderlein	On plants	1967	Flo, SCz, Sgo
Ectopsocidae			
Ectopsocus maindroni Badonnel	In stored products	1967	Gen, Isa, SCl, SCz
E. meridionalis Ribaga	On plants	1967	Isa, Pta, SCz, Sgo
E. richardsi Pearman	In stored products	1967	SCz
Peripsocidae			
Peripsocus pauliani Badonnel	On plants	1967	On 14 islands
P. stagnivagus Chapman	On plants	1967	On 13 islands
Pseudocaecillidae			
Pseudocaecilius criniger Perkins	In stored products?	1967	Esp, Flo, Isa, Pon, SCz, Sgo
P. tahitiensis Karny	In stored products ?	1967	Isa, Rab, SCl, SCz, Sgo, Sey

(continued)

Table 1. *(continued)*

Scientific name and Common name[a]	Probable mode of introduction of the species[b]	First record[c]	Known on Island
Archipsocidae			
Archipsocus spinosus Thornton	In stored products?	1967	Isa, Pta, SCl, SCz, SFe, Tor
Phthiraptera (lice)			
Polyplacidae			
Polyplax spinulosa (Burmeister)	On rats	1923	Flo
Thysanoptera (thrips)			
Merothripidae			
Merothrips morgani Hood	On plants	1989	Isa, SCz
Thripidae			
Franklinella rodeos Moulton	On plants	1989	SCz, Pon
Heliotrips haemorrhoidalis (Bouché), the greenhouse thrips	On plants	1989	Isa, Pon, SCl, SCz, Sgo
Scolothrips pallidus Beach	On plants	1989	SCz
Thrips sp.	On plants	1989	SCz
Phlaeothripidae			
Haplothrips gowdeyi Franklin, black flower thrips	On plants	1989	Fer, Flo, Gen, Isa, Pon, Rab, SCz
Karnyothrips, near *longiceps* (Hood)	On plants	1989	SCz, Sgo
Strepterothrips floridanus Hood	On plants	1989	Fer, Flo, Isa, Pon, SCl
Hemiptera (true bugs)			
Miridae, plant bugs			
Engytatus modesta (Distant)	On plants	1991	Fer, Flo, Isa, Pon, SCz, Sgo
Horcias lacteiclavus Distant	On plants	1964	SCz
Stnenaridea vulgaris (Distant)	On plants	1992	Fer, Isa, SCz, Sgo
Taylorilygus pallididulus Blanchard	On plants	1964	SCl, SCz
Tytthus parviceps (Reuter)	On plants	1970	SCz
Cimicidae			
Cimex lectularis L., bed bug	On bedding	1925	Flo
Anthocoridae, minute pirate bugs			
Alofa sodalis (White)	On plants	1964	SCz
Amphiareus constricta (Stål)	On plants	1964	SCz
Lygaeidae			
Prytanes confusus (Barber)	On plants?	1989	SCz
Pyrrhocoridae, cotton stainer bugs			
Dysdercus concinnus Stäl	On plants	1925	SCz
D. lunulatus Uhler	On plants	1964	SCl
Reduviidae			
Barce fraterna (Say)	On plants	1996	SCz
Rasahus hamatus (F.)	On plants	1989	Esp, Flo, Isa, SCl, SCz
Tagalis seminigra Champion	On plants	1995	SCz
Pentatomidae, stink bugs			
Alcaeorrhynchus grandis (Dallas)	On plants	1934	Flo
Loxa viridis (Palisot de Beauvois)	On plants	1991	Flo, Isa, SCz
Homoptera (leaf hoppers and scale insects)			
Aleyrodidae, whiteflies			
"*Aleyrodes* sp"	On plants	1989	Isa, SCz, Sgo
Cicadellidae, leaf-hoppers			
Agallia sp.	On plants	1989	Fer, Isa, SCz, Sgo
Balclutha aridula Linnavuori	On plants	1989	Fer, Isa, Rab, Sgo
B. incisa (Matsumura)	On plants	1990	Fer, SCz
B. lucida (Butler)	On plants	1989	On 8 islands
B. neglecta (DeLong & Davidson)	On plants	1989	Fer, Isa, Pin
Circulifer tenellus (Baker)	On plants	1989	On 13 islands
Coelidiana sp.	On plants	1990	Isa, SCz
Empoasca canavalia DeLong	On plants	1989	On 10 islands
Macrosteles fascifrons (Stål)	On plants	1989	Isa, SCz, Sgo, SCl
Sanctus discalis (Van Duzee)	On plants	1933	Fer, Flo, Mar, Pta, Sgo
Scaphytopius obliquus (Walker)	On plants	1995	Fer, Isa, Pon, SCl, SCz, Sgo
Xestocephalus desertorum (Berg)	On plants	1989	On 9 islands
Delphacidae, plant hoppers			
Caenodelphax teapae Fowler	On plants	1964	SCz
Peregrinus maidis (Ashmead)	On plants	1964	SCz
Sogatella kolophon Kirkaldy	On plants	1964	SCl, SCz

Table 1. *(continued)*

Scientific name and Common name[a]	Probable mode of introduction of the species[b]	First record[c]	Known on Island
Syndelphax dissipatus Muir	On plants	1964	SCz
Aphididae (*s.latu.*), aphids			
Acyrthosiphon bidenticola Smith	On plants	1991	Fer, SCz
Aphis coreopsidis (Thomas)	On plants	1991	Fer, Isa, SCz, Sgo
A. craccivora Koch, cowpea aphid	On plants	1991	Fer, Isa, SCz, Sgo
A. gossypii Glover, cotton aphid	On plants	1991	Fer, Isa, Mar, SCz, Sgo
A. nerii Boyer de Fonscolombe, oleander aphid	On plants	1991	Fer, Isa, Pta, SCz, Sgo
A. spiraecola Schouteden, green citrus aphid	On plants	1991	Esp, Fer, Isa, SCz, Sgo
Aulacorthum circumfleuxum (Buckton)	On plants	1992	Isa
A. solani (Kaltenbach)	On plants	1991	SCz
Cerataphis sp.	On plants	1991	Sgo
Hysteroneura setariae (Thomas)	On plants	1991	On 8 islands
Myzus persicae (Sulzer), green peach aphid	On plants	1991	Fer, SCz
Pentalonia nigronervosa Coquerel, banana aphid	On plants	1991	SCz
Rhopalosiphum maidis (Fitch), corn leaf aphid	On plants	1991	Isa, SCz, Sgo
R. rufiabdominale (Sasaki)	On plants	1991	Isa, SCz
Scale Insects			
Margarodidae			
Icerya purchasi Mashell, the cottony cushion scale	On plants	1983	Bal, Flo, Isa, SCl, SCz, Sey, Sgo
Ortheziidae, the ensign scales			
Orthezia insignis Bourne, greenhouse orthesia	On plants	1975	SCl
Pseudococcidae, the mealy bugs			
Ferrisia virgata (Cockerell), striped mealybug	On plants	1975	Bal, Isa, Sgo, SCz
Geococcus coffeae Green	On plants	1975	SCz
Planococcus citri (Risso), citrus mealybug	On plants	1975	SCl, SCz
Coccidae, the scale insects			
Coccus hesperidium L., brown soft scale	On plants	1902	Bal, Isa, Pta, Sey
C. viridis (Green), green scale	On plants	1975	SCz
Parasaissetia nigra (Nieter), nigra scale	On plants	1975	SCz, Pla
Pulvinaria urbicola Cockerell	On plants	1975	Scz
Saissetia coffeae (Walker), hemispherical scale	On plants	1975	Isa, SCl, SCz
S. miranda (Cockerell & Parrott), Mexican black scale	On plants	1975	SCl
S. neglecta DeLotto, Caribbean black scale	On plants	1975	Bar, Pla
Asterolecaniidae, the pit scales			
Asterolecanium pustulans (Cockerell), oleander pit scale	On plants	1975	Isa
A. puteanum Russell	On plants	1975	Isa
Diaspididae, the armored scales			
Aspidiotus destructor Signoret, coconut scale	On plants	1975	SCz
Hemiberlesia lateniae (Signoret), lantana scale	On plants	1975	Bal, Isa, Sgo, SCz, Pta
Howardia biclavis (Comstock), mining scale	On plants	1975	Sgo, SCl, SCz
Melanaspis odontoglossi (Cockerell)	On plants	1902	Isa, Sgo, SCz
Parlatoria crotonis (Douglas)	On plants	1975	SCz
Pseudaulacaspis major (Cockerell)	On plants	1975	Sgo
Selenaspidis articulatus (Morgan)	On plants	1975	Sgo, SCl, SCz
Coleoptera (beetles)			
Hydrophilidae, water scavenger beetles			
Aculomicrus sp	In debris	1989	Isa
Dactylosternum abdominale F.	In debris	1989	SCz
D. sp.	In debris	1989	Isa
Ptiliidae, feather wing beetles			
Acrotrichis discoloroides Johnson	In debris	1989	SCz
Staphylinidae, rove beetles			
Atheta coriaria (Kraatz)	In debris	1985	Flo, Isa, SCl, SCz
Myrmecocephalus cingulatus (Erichson)	In debris	1989	SCl, SCz
Oligota chrysopyga Kraatz	In debris	1985	Isa, SCl, SCz
Phanerota sp.	In debris	1985	SCz
Piestus pygmaeus Laporte	In debris	1985	SCz
Scarabaeidae, scarab beetles			
Ataenius gracilis (Melsheimer)	In soil (dung)	1991	SCz

(continued)

Table 1. *(continued)*

Scientific name and Common name[a]	Probable mode of introduction of the species[b]	First record[c]	Known on Island
Dermestidae, dry skin beetles			
Dermestes ater DeGeer, black larder beetle	In stored products	1985	On most islands
D. carnivorus F.	In stored products	1899	Dar, Esp, Isa, SCl, SCz
D. maculatus DeGeer, hide beetle	In stored products	1835	On 8 islands
Anobiidae, death-watch beetles			
Stegobium paniceum (L.), drugstore beetle	Stored products	1985	SCz
Bostrichidae, branch and twig borers			
Dinoderus minutus (F.), bamboo powderpost beetle	Dry wood	1985	SCz
Lyctus brunneus Stephens	Dry wood	1964	SCz
Minthea rugicollis (Walker)	Dry wood	1985	SCz
Sinoxylon conigerum Gerstäcker	Dry wood	1996	Flo
Trogoxylon sp.	Dry wood	1985	SCz
Cleridae, checkered beetles			
Necrobia rufipes DeGeer, redlegged ham beetle	Stored products	1835	On 8 islands
Tarsostenus univittatus (Rossi)	Dry wood?	1985	SCz
Nitidulidae, sap beetles			
Brachypeplus sp.	Fruits?	1985	SCz, SCl
Carpophilus dimidiatus (F.), corn sap beetle	Stored products?	1985	Flo, SCl, SCz
Stelidota sp. A	Fruits?	1985	Isa, Mar, Pta, SCl, SCz, Sgo
Urophorus humeralis (F.), pineapple beetle	Stored products?	1985	Isa, SCz
Silvanidae, flat bark beetles			
Monanus concinulus Walker	Stored products	1985	SCz
Oryzaephilus surinamensis L., sawtoothed grain beetle	Stored products	1985	SCz
Silvanus difficilis Halstead	Stored products	1991	SCz
Laemophloeidae, flat bark beetles			
Cryptolestes klapperichi Lefkovitch	Stored products	1985	Esp, Flo, Gen, Isa, SCl
Laemophloeus suturalis Reitter	Stored products	1985	Scz
Cerylonidae, cerylonid beetles			
Euxestus erithacus Chevrolat	In detritus or debris	1985	Isa, SCl, SCz, Sgo
Coccinellidae, ladybird beetles			
Coccidophilus sp.	On plants (predator on scales)	1985	Flo, SCz
Lathridiidae, minute brown scavenger beetles			
Adistemia watsoni (Wollaston)	Stored products	1985	Isa
Cartodere constricta (Gyllenhal), plaster beetle	Stored products	1985	Flo, Isa, SCl, SCz
Dienerella filum (Aubé)	Stored products	1985	Isa
Mycetophagidae			
Typhaea stercorea L., hairy fungus beetle	Stored products	1989	Isa, Rab, SCz
Tenebrionidae, darkling beetles			
Alphitobius laevigatus (F.), black fungus beetle	Stored products	1904	Flo, Scz
Gnathocerus cornutus (F.), broadhorned flour beetle	Stored products	1899	Flo, Isa, SCz, SFe, Sgo
G. maxillosus (F.), slenderhorned flour beetle	Stored products	1964	Isa, SCz, Sgo, SFe
G. sp.	Stored products	1964	SCz
Lobopoda galapagoensis Linell (?)	In dry (fire?) wood	1898	Fer, Flo, Isa, SCz
Sitophagus hololeptoides (Laporte)	Stored products	1975	Isa, SCz, SFe
Tribolium castaneum Herbst, red flour beetle	Stored products	1964	SCz
Anthicidae, ant like flower beetles			
Omonadus floralis (L.)	In stored products	1989	SCz
Cerambycidae, long-horned wood boring beetles			
Aerenea quadriplagiata Boheman	Construction wood?; not established	1975	SCz
Eburia pilosa (Erichson)	Construction wood ?	1964	Isa, SCl, SCz, Sgo
Nesoeme kuscheli Linsley & Chemsak	Construction wood ?; not established	1964	SCz
Bruchidae, seed beetles			
Acanthoscelides obtectus (Say), bean weevil	Stored products	1989	SCz
Amblycerus piurae (Pierce)	Stored products	1927	SCz, Pon
Zabrotes subfasciatus Boheman, Mexican bean weevil	Stored products	1985	SCz
Chrysomelidae, leaf beetles			
Chaetocnema confinis Crotch	On plants	1985	Fer, Isa, SCz, Sgo
Anthribidae, fungus weevils			
Araecerus fasciculatus (DeGeer), coffee bean weevil	Stored products	1985	Flo, Isa, SCl, SCz

Table 1. *(continued)*

Scientific name and Common name[a]	Probable mode of introduction of the species[b]	First record[c]	Known on Island
Scolytidae, bark beetles			
Coccotrypetes carpophagus (Hornung)	In seeds or nuts	1989	SCl
C. rhizophorae (Hopkins)	In plants or seeds	1985	Isa, SCz
C. dactyliperda (F.)	In seeds or nuts	1991	SCz
Pagiocerus frontalis F.	In seeds or maize	1964	SCz
Curculionidae, weevils			
Caulophilus oryzea (Gyllenhal), broadnosed grain weevil	Stored products	1985	SCz
Eubulus sp.	On plants	1992	SCz
Metamasius hemipterus (L.), West Indian cane weevil	On plants	1985	SCz
Semnorhynchus sp.	On plants	1991	SCl
Sitophilus oryzae (L.), rice weevil	Stored products	1985	Esp, SCz
Lepidoptera (moths)			
Tineidae, clothes moths			
Erechtias minuscula (Walsingham)	Dead plants	1989	Esp, Isa, Mar, SCl, SCz
Trichophaga tapetzella L.	Stored products	1966	Fern, SFe
Xylesthia pruniramiella Clemens	Stored products	1966	On 8 islands
Tortricidae, tortricid moths			
Bactra philocherda Diakonoff	On plants	1989	SCz, Sgo
Crocidosema plebejana Zeller	On plants	1923	Bal, Isa, SCz
Episimus transferranus (Walker)	On plants	1989	Isa
Strepsicrates smithiana (Walsingham)	On plants	1923	Bal
Pterophoridae, plume moths			
Exelastis cervinicolor (Barnes & McDunnough)	On plants	1923	On 11 islands
Exelastis pumilio (Zeller)	On plants	1992	Isa, Rab
Lantanophaga pusillidactyla (Walker), lantana plume moth	On *Lantana*	1923	Gen, Isa, Mar, SCz
Megalorhipida defectalis (Walker)	On plants	1923	On 10 islands
Stenoptilodes brevipennis (Zeller)	On plants?	1989	Isa, SCz
Hesperiidae, skippers			
Calpodes ethlius (Cramer), the larger canna leaf roller[d]	On *Canna edulis*	1987	Isa
Lycaenidae, hairstreak and blue butterflies			
Hemiargus ramon (Dognin)	On plants	1995	Bal, Esp, Flo, Isa, SCl, SCz, Sgo
Pyralidae, snout moths			
Phycitinae			
Ancylostomia stercorea (Zeller)	Stored beans	1989	Gen, Isa, Pta, SCz, Sgo
Etiella zinckenella (Treitschke), lima bean pod borer	Stored products	1906	On 9 islands
Fundella argentina Dyar	Stored beans	1965	Isa, SCl, SCz, Sgo
Hypsipyla grandella (Zeller), mahogany shoot borer	On plants (*Cedrela*)	1960	SCl, SCz
Crambidae, grass moths			
Agathodes designalis Guenée	On plants	1989	Isa, SCz, Sgo
Asciodes gordialis Guenée	On cassava	1906	On 11 islands
Caprinia perinsalis Walker, tobacco leaf-folder[d]	On plants	1989	Isa, Pta, SCl, SCz, Sgo
Diaphania hyalinata (L.), melon borer[d]	On cucurbits	1932	Bal, Isa, Mar, Pta, SCz
D. indica (Saunders), melon moth	On cucurbits	1964	SCl, SCz
Herpetogramma bipuntalis (F.)[d]	On plants	1992	Gen, Isa, SCz, Sgo
H. phaeopteralis (Guenée)	On Poaceae	1970	Isa, SCl, SCz, Sgo
Hymenia perspectalis (Hübner)[d]	On plants	1906	Esp, Isa, Pta, SCl, SCz, Sgo
Lineodes integra (Zeller)	On Solanaceae	1989	Isa, Pta, Sgo
Marasmia trapezalis (Guenée), maize webworm	On Poaceae	1992	Isa, SCz, Sgo
Omiodes indicata (F.)	On plants	1989	Isa, Pta, SCz, Sgo
Penestola bufalis (Guenée)	On plants	1906	On 9 islands
Pilocrocis ramentalis Lederer[d]	On plants	1899	Isa, SCl, SCz, Sgo
Pyrausta panopealis (Walker)	On plants?	1989	On 9 islands
Samea ecclesialis Guenée[d]	On plants?	1964	Isa, SCl, SCz, Sgo
Sisyracera inabsconsalis (Möschler)	On plants?	1989	Isa, SCl, SCz
Spoladea recurvalis (F.), beet webworm[d]	On plants	1906	Esp, Flo, Isa, SCl, SCz, Sgo
Syngamia florella (Cramer)	On Rubiaceae	1906	Flo, Gen, Isa, SCl, SCz, Sgo
Terastia meticulosalis Guenée[d]	On *Erythrina*	1964	Pta, SCz
Geometridae, inchworm moths			
Disclisioprocta stellata (Guenée)[d]	On plants	1923	On 12 islands

(continued)

Table 1. *(continued)*

Scientific name and Common name[a]	Probable mode of introduction of the species[b]	First record[c]	Known on Island
Hydria affirmata (Guenée)	On ships	1969	Isa, SCl, SCz, Sgo
Sphacelodes vulneraria (Hüber)[d]	On ships	1964	SCz
Noctuidae, owlet moths			
Bagisara repanda (F.)	On Malvaceae	1970	Isa
Eublemma recta (Guenée)	In Covolvulaceae seeds	1975	Gen, Isa, Mar, Pta, SCz, Sgo
Heliocontia margana (F.)	On Malvaceae	1923	On 12 islands
Heliothis cystiphora (Wallengren)	On Poaceae?	1923	On 14 islands
Paectes arcigera (Guenée)	On Burseraceae	1923	On 16 islands
Ponometia indubitans (Walker)	On Sterculiaceae	1975	Esp, Gen, Isa, SCl, SCz
Diptera (flies)			
Psychodidae, moth flies			
Clogmia albipunctata (Williston)	Rotting plant matter	1985	SCz
Psychoda alabangensis del Rosario	Rotting plant matter	1985	SCz
P. savaiiensis Edwards	Rotting plant matter	1985	Isa, SCl
Culicidae, mosquitos			
Culex pipiens quinquefasciatus Say, southern house mosquito	Larvae in water	1989	SCl, SCz
Simuliidae, black flies			
Simulium bipunctatum Malloch	On plants (aquatic)?	1989	SCl
Ceratopogonidae, biting midges			
Culicoides pusillus Lutz	Plant debris	1964	SCz
Forcipomyia genualis (Loew)	Plant material	1964	Dar, Flo, Isa, SCz, SFe
Bombyliidae, bee flies			
Mythenteles sp.	Soil?	1985	On 8 islands
Phoridae, humpbacked flies			
Dohrnophora cornuta Bigot	Soil	1925	Bal, Flo, Isa, SCz, Sgo
Megaselia scalaris (Loew)	Soil	1923	Esp, Flo, Gen, Isa, SCl, SCz
Syrphidae, flower flies			
Ornidia obesa (Fabricius)	Wet soil or semi-liquid waste	1989	Isa, SCl
Tephritidae, fruit flies			
Anastrepha fraterculus (Wiedemann)	Fruits	1989	Cam, Dap, Flo, SCl, SCz
Piophilidae, skipper flies			
Piophilia casei (Linnaeus), cheese skipper	Food products	1835	Flo, SCz
Milichiidae, milichiid flies			
Desmometopa m-nigrum Zetterstedt	Soil or debris	1925	Bal
D. tarsalis Loew	Soil or debris	1983	Not reported
D. varipalpis Malloch	Soil or debris	1983	Isa
Sepsidae, black scavenger flies			
Palaeosepsis armillata (Melander & Spuler)	Debris or dung	1992	Isa
Sphaeroceridae, small dung flies			
Coprica hirtula (Rondani)	Soil or debris	1964	Fer, SCz, Wol
Drosophilidae, vinegar flies			
Drosophila (D.) hydei Sturtevant	Fruits	1977	Isa, SCz
D. (D.) immigrans Sturtevant	Fruits	1925	Flo, Sgo
D. (D.) repleta Wollaston	Fruits	1977	SCz
D. (Scaptodrosophila) latifasciaeformis Duda	Fruits	1977	SCz
D. (Scophophora) ananassae Doleschale	Fruits	1977	SCz
D. (S.) melanogaster Meigen	Fruits	1977	SCz
D. (S.) simulans Sturtevant	Fruits	1948	Bal, Isa, SCl, SCz
Gitona braziliensis Lima	On citrus plants (parasitoid on scales)	1948	SCz
Ephydridae, shore flies			
Clasiopella uncinata Hendel	Saline soil or mangrove debris	1989	SCz
Hecamede brasiliensis Cresson	Saline soil or mangrove debris	1989	Flo, Isa
Fanniidae			
Fannia canicularis (L.), little house fly	Manure or soil	1899	Isa
Fannia pusio (Wiedemann), chicken dung fly	Manure or soil	1932	Flo, Isa, SCl, SCz, SFe
Muscidae, house flies, and so on.			
Atherigona orientalis Schiner	Soil or fruits	1899	Esp, Flo, SCl, SCz
Hydrotaea aenescens (Weidemann)	Spoiled food	1899	Bal, Fer, Flo, Isa, SCz
Musca domestica L., house fly	Spoiled food	1925	Bal, Flo, Isa, SCl, SCz
Stomoxys calcitrans (L.), stable fly	Cattle manure	1925	Bal, Flo, Isa, SCl, SCz
Synthesiomyia nudiseta (Wulp)	Spoiled food	1925	Flo, Isa, Rab, SFe, SCz

Table 1. *(continued)*

Scientific name and Common name[a]	Probable mode of introduction of the species[b]	First record[c]	Known on Island
Calliphoridae, blow flies			
Chrysomya albiceps (Wiedemann)	Spoiled food	1985	Esp, Flo, Isa, SCl, SCz, SFe
C. megacephala (F.)	Spoiled food	1989	Caa, Isa, SCz
Cochliomyia macellaria (F.), secondary screw worm	Livestock	1835	Esp, Flo, Isa, Pon, SCl, SCz, SFe
Sarcophagidae, flesh flies			
Blaesoxipha plinthopyga (Wiedemann)	Manure or soil	1905	Flo, SCl, SCz, SFe
Siphonaptera (fleas)			
Tungidae			
Tunga penetrans L., chigoe fleas	In pigs	1947	Flo, Sgo
Pulcidae			
Ctenocephalides felis (Bouché), cat flea	On cats	1989	SCz, Sgo
Pulex (irritans Linnaeus?), human flea	On dogs	1989	Sgo
Hymenoptera (wasps and ants)			
Ichneumonidae, ichneumon wasps			
Diplazon laetatorius F.	Parasitoid in insects	1985	Isa
Venturia canescens Gravenhorst	Parasitoid in insects	1985	SCz
Aphelinidae			
Aphytis acutaspidis Rosen and DeBach	Parasitoids of hard scales	1991	Rab, Sgo
Archenomus imitatrix (Fullaway)	Parasitoids of whiteflies	1991	Fer, Isa, SCz
Centrodora mireyae (DeSantis)	Parasitoids of eggs	1991	SCz
C. perkinsi (Waterston)	Parasitoids of eggs	1991	Fer, Isa, SCz
Coccophagus rusti Compere	Parasitoids of soft scales	1991	Isa, SCz, Sgo
Encarsia diaspidicola (Silvestri)	Parasitoids of hard scales	1991	Esp
Encarsia citrina Crawford	Parasitoids of hard scales	1991	Sgo
Encarsia pergandiella Howard	Parasitoids of whiteflies	1991	Isa, Rab, SCz, Sgo
Eucharitidae			
Orosema costaricensis W and W	As eggs on bananas	1991	SCz
Chalcididae, chalcidoid wasps			
Brachymeria podagrica F.	Parasitoid of fly pupae	1991	Flo, Isa, SCz, SCl, Sfe
Conura femorata Walker	Parasitoid of lepidoptera pupae	1991	Isa, San, SCz, Sgo
Pteromalidae			
Spalangia cameroni Perkins	Parasitoids of fly pupae	1991	Isa, SCz, Sgo
S. drosophila (Ashmead)	Parasitoids of insect pupae	1991	Scz, Pon
S. endius Walker	Parasitoids of fly pupae	1839	Isa [?James = type locality]
Encyrtidae, chalcidoid wasps			
Apoanagyrus trinidadensis Kerrich	Parasitoid in mealybugs	1991	Isa, SCz
Cheiloneurus elegans elegantissimus DeSantis	Parasitoids of mealybugs	1991	Isa, Pon
Evaniidae, ensign wasps			
Evania appendigaster L.	Parasitoid of cockroach eggs	1989	Scz
Scelionidae			
Macrotelia absona	Parasitoids of orthoptera eggs	1991	Isa, SCz
Trissolcus teretis Johnson	Parasitoids of lepidoptera eggs	1991	Isa, Sgo
Formicidae, ants			
Monomorium floricola Jerdon	On plants or soil	1924	Flo, Gen
M. pharaonis L., pharaoh ant	On plants or soil	1985	Pta, SCz
Solenopsis geminata (F.), fire ant	On plants or soil	1906	Flo
S. globularia (F. Smith)	On plants or soil	1906	Gen, Isa, Dap, SCz
S. saevissima (F. Smith)	On plants or soil	1985	SCz
Tapinoma melanocephalum F.	On plants or soil	1985	Esp, Gen, SCz, SCl
Tetramorium simillimum F. Smith	On plants	1985	Flo, Sgo
Wasmannia auropunctata Roger, little red fire ant	On plants	1905	On many islands
Vespidae, wasps			
Polistes v. versicolor (Olivier)	With fruits on ships	1988	On most islands
Brachygaster lecheguana (Latreille)	With fruits on ships?	1994	Scz

Bal, Baltra; Bar, Bartholome; Caa, Caamano; Cam, Campeon; Dap, Daphne Major; Esp, Espanola; Fer, Fernandina; Flo, Floreana; Gen, Genovesa; Isa, Isabela; Mar, Marchena; Pla, Plaza; Pon, Pinzon; Pta, Pinta; Rab, Rabida; SCl, San Cristobal; SCz, Santa Cruz; Sey, Seymour Norte; Sfe, Santa Fe; Sgo, Santiago; Wol, Wolf.

[a]Common names from the Entomological Society of America (ESA 1989).

[b]Based on the biology and habitat preferences of adults and immatures.

[c]Year of first collection of species from Galápagos or first publication of it if collection date not given.

[d]Denotes species known to be migratory.

Table 2. Galapagos insect orders containing introduced species with total number of all species, introduced species, and percent of introduced species (modified from Peck 1996a)

Order	Total known insect species (*N*)	Introduced species (*N*)	Introduced % species
Diplura	2	1	50.0
Thysanura	3	1	33.3
Orthoptera	32	4	12.5
Blattaria	18	11	61.1
Dermaptera	7	4	57.1
Embidiina	2	1	50.0
Psocoptera	40	13	32.5
Phthiraptera	80	1	1.3
Thysanoptera	50	8	16.0
Hemiptera	130	16	12.3
Homoptera	139	52	37.4
Coleoptera	419	61	14.6
Lepidoptera	298	46	15.4
Diptera	237	39	16.5
Siphonaptera	4	3	75.0
Hymenoptera	253	31	12.3

(continued from page 222)
identified. The modes of introduction have been by a variety of methods (Table 3). The relative abundance of species by island is summarized in Table 4. The rate of accumulation of these species is shown in Table 5 and Fig. 5.

Discussion

There is no compelling evidence that the islands were known by the pre-Columbian inhabitants of South America. Although the islands may have been visited by Inca peoples from coastal Ecuador or Peru, there was no long-term habitation of the Galápagos by these people (Hickman 1985). The first European landings were Bishop Tomas de Berlanga and his crew in 1535, and the first insect introductions may have arrived at that time in the form of cockroaches, dermestid beetles, and *Necrobia* (clerid) beetles. These were all associated with humans and stored products in sailing ships. Pirates or whalers may have brought an alleculid beetle (and maybe other drywood insects such as anobiid or scolytid beetles) in logs or firewood from the mainland from the 1600s to the early 1800s. Permanent human settlement started in the 1830s and most introductions must date from this period and later.

Identifications, Establishment, and Extirpations. Some of the species listed in Table 1 may be open to doubt. Some records may be based on errors in identification. We were not able to confirm some of the old records and have accepted them as they stand in the literature.

Species based on only a single record may have failed to become established. An example is the bedbug (*Cimex lectularis* L.) reported in 1925. To the best of our knowledge, it has not been collected since.

Some records probably are spurious, such as the record of the rice weevil (*Sitophilus oryzae* L.) on Espanola, which was probably carried by a field party to Espanola. It probably is not established in the wild because there are no other records of it.

Some species may have been extirpated. The secondary screw worm [*Cochliomyia*

Fig. 4. Typical mixed crop agriculture of a small farm on Santa Cruz Island. Visible here are coffee, papaya, cassava, banana, and a weedy understory of introduced *Bidens* (Compositae).

macellaria (F.)] was first reported in 1835 and last found in 1970. It may have been replaced by the more recently introduced fly *Chrysomya albiceps* (Wiedemann), which was first collected in 1985.

Taxonomic Distribution of Introduced Species. By definition, oceanic islands are isolated, and the species proportions in their faunas do not correspond with those in continental areas. This is a phenomenon of island isolation and is called "disharmonic" or "unbalanced" faunal representation (Carlquist 1965, 1974). The Galápagos insect fauna is unbalanced naturally. Some insect orders are absent, and others have a low species representation because of the natural difficulties the species in these orders have with dispersal or colonization. Human transport partially helps to overcome the natural infrequency of dispersal in these latter species and can lead to a disproportionate representation of introduced species (Table 2). As examples, 50% or more of the species in the orders Diplura, Blattaria, Dermaptera, Embidiina, and Siphonaptera are introduced.

Large orders such as Coleoptera, Homoptera, Lepidoptera, Diptera, and Hymenoptera have the greatest total numbers of introduced species.

Modes of introduction. Most of the introduced species are plant-feeding insects such as thrips, aphids, small moths, leafhoppers, and scale insects (Table 3). These most likely arrived on their host plants (Fig. 6). Exactly how many species of these really occur remains unknown because of incomplete taxonomic study, and many of these are in taxonomically difficult groups. Interestingly, some of these phytophagous insects apparently have carried their predators or wasp parasitoids with them. Examples are the *Gitona* fly and chalcid and encyrtid wasps.

Schreiner (1991) found that most insect introductions to the island of Guam came on ornamental plants and flowers. As currently understood, 48% of the insects introduced into the Galápagos probably arrived on living plants (Table 3). Soil on plant roots certainly has introduced earthworms, millipedes, centipedes, terrestrial isopods, symphylans, silverfish, and some beetles and ants. Other modes occur in lower frequency. A tiger beetle (*Cicindella trifasciata* F.) seems to have arrived during or following the 1982-1985 El Niño event, and Desender et al. (1992) think this was caused by human agency but do not say how or why. We are inclined to think that it was a natural dispersal and have not placed it in our list. El Niños are climatical times most suited for the natural dispersal of insects to and between the islands (Peck 1994a, b) and most suited to promote establishment of the colonists.

Table 3. Numbers of insects probably introduced to the Galápagos by their most likely modes of human transport

Mode	*n*
On living plants	139
In dry stored agricultural and food products	42
In plant debris and soil around plants	37
Parasitoids of (introduced?) insect hosts	20
In fresh or spoiled fruits, vegetables and food products	19
In dry goods, dunnage, pallets, and packaging materials	12
In dry wood, construction materials, and logs	10
On ships in general	6
On livestock and pets	4
On rats	1
Human ectoparasites, probably in bedding or clothing	1
In water containers (larvae, mosquitoes?)	1
Total	292

An important early mode of introducing soil arthropods to North America was the practice of loading earthen ballast into ships in European ports and unloading it on waste ground at North American ports (Lindroth 1957, Larson and Langor 1982). We have no evidence that earthen ballast was offloaded in the Galápagos.

Migrations. Some insects, such as locusts and dragonflies, are known to engage in long-distance migratory flights (Peck 1992). As stated by Ferguson et al. (1991), most Lepidoptera that are major field-crop pests in the temperate zones, and probably also in the tropics, are also long-range migrants. As many as 27 additional species of Noctuidae in the genera *Agrotis, Anomis, Anticarsia, Argyrogramma, Ascalapha, Callopistria, Celiptera, Characoma, Gonodonta, Heliothis, Hypena, Letis, Melipotis, Mocis, Mythimna, Ophiuche, Peridroma, Platysenta, Pseudaletia, Pseudoplusia,* and *Spodoptera* are present in the Galápagos (see Hayes 1975 for species names) and either are known to be long-range migrants or probably are long-range migrants (J. D. Lafontaine, personal communication). Most of these are serious pests of various field crops. At times, they may have reached the archipelago either naturally or with human assistance and with or after the establishment of their crop host. We have taken a conservative approach and have not placed them in our list of introductions. However, it is possible that some of the species that we have listed actually arrived by natural means, especially those that are

Table 4. Island distributions of introduced Galápagos insects that are known from seven or fewer islands

Island	Species (*n*)
Santa Cruz[a]	165
Isabela[a]	83
Floreana[a]	49
San Cristobal[a]	48
Santiago[b]	47
Fernandina	20
Pinta	12
Baltra[a]	10
Santa Fe	9
Espanola[b]	9
Genovesa	8
Rabida	5
Pinzon	3
Seymour (Norte)	2
Marchena	2
Darwin	2
Plaza	2
Daphne	2
Bartolome	1
Campion	1
Caamano	1
Wolf	1

[a] Present long-term human habitation.

[b] Past long-term human habitation.

Table 5. Decade of discovery of first records of insects introduced to the Galápagos Islands compared with growth of permanent human population and tourism visits (data from Ecuador National Census and Galápagos National Park Services)

Decade	Insects by decade	Cumulative total species	Human population	Tourist visits
1830–1839	4	4	—	—
1870–1879	2	6	—	—
1880–1889	1	7	—	—
1890–1899	8	15	—	—
1900–1909	14	29	600	—
1910–1919	1	30	600	—
1920–1929	24	54	650	—
1930–1939	4	58	700	—
1940–1949	3	61	1,000	1,000?
1960–1969	44	105	3,800	5,000?
1970–1979	31	136	4,000	36,000
1980–1989	99	235	10,000	144,000
1990–1996	57	292	14,000	333,000

known to be migratory on the east coast of North America (see Ferguson 1991); these are indicated in Table 1.

Places of Origin. Most insect introductions probably come from the continental mainland of Ecuador. This is the past and present source of most goods, building materials, foodstuffs, agricultural stocks, and of people who have traveled to the islands. Ecuadorian settlers in the Galápagos formerly brought uncontrolled amounts of agricultural goods, nursery stock, and plant cuttings with them. During World War II, several U.S. military bases and observation posts were supplied from Panama. Today, almost all consumer goods come from Ecuador, mostly by supply ship (Fig. 7), but a significant tonnage of fresh fruits and vegetables arrives by air freight. These supplies are for both the residents and the growing itinerant tourist population. Tourists, themselves, probably carry few insects, but their tour boats may aid in spreading insects between the islands (Silberglied 1978). The Galápagos National Park has a strict set of guidelines for residents, tourists, and scientists to avoid or eliminate the interisland transport of insects and plant seeds.

Islands of Introduction. A summary of the species numbers known from seven or fewer islands is given in Table 4. It is evident that the large and central islands (Santa Cruz, Isabela, Floreana, San Cristobal, and Santiago) that have (or have had) the most human activity and transport contact with the mainland have accumulated the most introduced species by accidental introduction. There are undoubtedly other unrecorded anthropophilic (human-associated) species on all these islands. Santiago was once colonized by humans but since has been abandoned. Espanola and northern and western Isabela were the former sites of now abandoned U.S. military posts in World War II.

There is a significant positive relationship between island area and number of naturally occurring (endemic plus native) insect species in the Galápagos (Peck 1996a), but this is not as significant for the introduced species. Santa Cruz has the largest number of introduced species but is by no means the largest island. Rather, it does have the largest human population and also is the best-studied island.

It is evident that some introduced species have been able to secondarily disperse (mostly

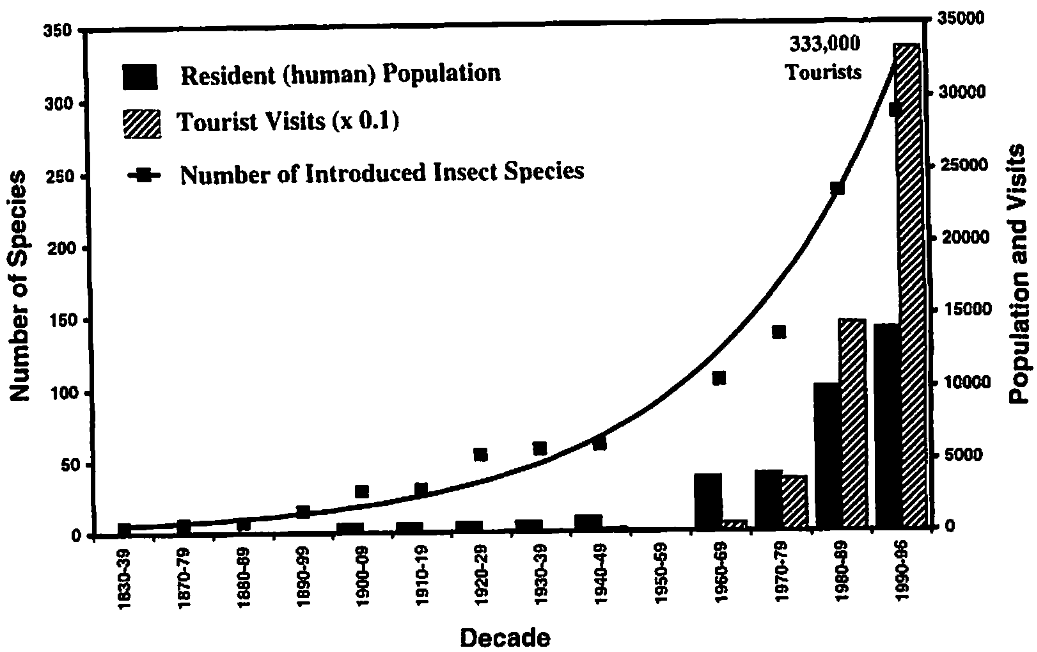

Fig. 5. Summary by decade of the cumulative discovery of first records of insects introduced to the Galápagos Islands compared with growth of the permanent human population and tourism visits (scaled to one-tenth). Population data from Ecuador National Census and Galápagos National Park Services. Line of increase of introduced insects: $r^2 = 0.9661$; $y = 4E\text{-}23e^{0.0288x}$.

Fig. 6. Yards of houses in the lowlands and highlands of the settled islands have a rich flora of introduced ornamental trees and shrubs. This yard has *Casuarina, Citrus, Hibiscus,* papaya, sugar cane, *Croton,* pineapple, and chenille plant. These all may have carried plant-feeding insects when they were brought from the mainland.

by wind?; see Peck 1994a) to the undisturbed outlying islands. For instance, Fernandina now is considered the world's most pristine large oceanic island, and it has never been settled by humans. Its 20 introduced species most likely have colonized from nearby and settled Isabela Island, which is upwind to prevailing air movements. Local fishermen, scientific parties, and tourism also may have partly aided the spread of species to the outer and smaller islands.

Accumulation of Introductions. Table 5 and Fig.5 illustrate the rate of accumulation of introduced species. These can show only when the species first were discovered and usually not when the actual introductions occurred. This especially is true for the parasitoid Hymenoptera, which were sought by J.H. in 1991. Note that the rate has been accelerating in the past three decades in concert with the growth of human population, commerce, and tourism (and, perhaps, with increased research

Fig. 7. Bulk goods are brought to the islands in cargo ships (left), but fresh produce now is carried as air freight. Passenger ships (right) have been implicated in distributing insects between islands when the insects are attracted to the ships' lights at night.

Fig. 8. The most conspicuous of the introduced insects is the wasp *Polistes versicolor*, which has spread throughout most of the lowland areas of most of the islands. This is a serious predator on Lepidoptera larvae and a competitor with insectivorous birds for these larvae.

activity). We cannot be sure that the real rate of introduction has increased, only that the rate of discovery has increased in the past three decades.

The rate of accumulation of introduced insects closely parallels the increase in both the population of human residents and the number of tourist visits per year (Fig. 5). The rate of increase has a good fit ($r^2 = 0.9661$) to an exponential relationship ($y = 4E - 23e^{0.0288x}$). Based on this relationship, we can predict that the number of introduced species could be 553 by the year 2010 and 1,749 by the year 2050. This exceeds the number of naturally occurring species now known from the Galápagos ($n = 1{,}530$; Table 2). The numbers of species able to establish may decrease as the number readily transported by humans begins to plateau and the carrying capacity of the islands to accept new immigrants is approached. However, if anything, our numbers represent an underestimate of the number of alien or tramp species already established on the islands that have either not been collected or not yet identified.

Impact of Introductions. The literature on island biology is filled with examples of change caused by introduced plants and vertebrates (Carlquist 1974). The biological impact of most of the introduced insect species on the Galápagos biotas and ecosystems is poorly known. Some species, such as the microhymenopteran parasitoids and the ensign wasp *Evania appendigaster* L., the latter which appeared in 1992 and exclusively parasitizes the oothecae (eggcases) of the introduced and abundant *Periplaneta* cockroaches (Peck and Roth 1992), may be beneficial in biological control.

Species invasions of continental habitats rarely are accompanied by the total exclusion of native competitors. The idea of biotic saturation predicts that alien species should not easily invade an intact community, especially on continents. However, island systems are more vulnerable because they seemingly are less saturated or the native species seemingly are "less competitive" (Simberloff 1986). Our impressions are that urban and agricultural disturbed areas in the Galápagos harbor the majority of the alien species, and that these are the places where there is less competition with the naturally occurring species.

We still do not know how many species have invaded natural habitats and how many plant-feeding species have moved onto the native vegetation. There is an urgent need to answer such questions so that proper management and protection methods can be developed. We know that the cockroach *Periplaneta australasiae* (F.) is now an abundant and widespread species and, perhaps, is the dominant, insect scavenger in arid-zone forests of most islands.

Some insect species are spreading actively. The cockroach *Anaplecta lateralis* (Burmeister) was found only in lowland arid zone habitats in 1991 (Peck and Roth 1992) but by 1996 had spread up to the *Miconia* humid shrub zone at 500 m on Santa Cruz. The cricket *Anaxipha* sp. appeared in 1970 and since then has been spread, probably by ships, throughout the islands of the Archipelago (Peck 1996b).

There are many examples of dramatically altered ecosystems on many tropical islands, including Hawaii (Howarth 1985). The most important effects of introduced species seem to stem from predation or habitat modification (Simberloff 1981). Competitive interactions between species rarely determine the success or failure of colonizing species entirely (Groves and Burden 1986, Kornberg and Williamson 1987, Mooney and Drake 1987). Most of the introduced species in the Galápagos seem to have had a neutral effect on the natural ecosystems, but the following five clearly have been harmful: (1) The little red fire ant, *Wasmannia auropunctata* Roger, has been the most harmful arthropod introduction to date and has had a very serious negative impact on populations of both endemic and native arthropods (Lubin 1984). At least seven other ant species probably have been introduced by humans (Meier 1994); their impact is unknown. (2) The vespid wasp *Polistes versicolor versicolor* (Olivier), introduced in 1988, now has spread to all but the northern tier of islands (Fig. 8). This is a voracious predator on insect larvae such as moth caterpillars, which are also a food source for many endemic birds such as some of Darwin's finches, and on larvae and adults of endemic *Calosoma* carabid beetles. From plague-like numbers in 1991, the populations seem to have settled back to lower numbers. (3) The vespid wasp *Brachygaster lecheguana* (Latreille) appeared on Santa Cruz in 1992 and is another new predator on the naturally occurring insects. Its stings are a nuisance to humans. (4) The black fly *Simulium bipunctatum* Malloch has become a severe nuisance to humans in the moist uplands of Isla San Cristobal since its introduction in 1990 (Abedrabbo et al. 1993). It may change the characteristics of the island's only stream ecosystem (Gerecke et al. 1995). (5) The cottony cushion scale, *Icerya purchasi* Malloch, reached pest proportions on several species of arid and littoral zone trees on Santa Cruz Island in 1995. It may lead to the premature death of these trees, which could alter forest tree species composition.

Prospects. For the protection of the integrity of the Galápagos ecosystem, future introduction of insect species must be prevented. In the past, most of the introductions were by boats and ships (Fig. 7). The last two decades have seen a decline in ship transport to the islands, but a dramatic increase in tourism and transport of goods by aircraft. It now is evident that even more new species can be carried accidentally to the Galápagos on aircraft (see Laird 1951, Dale and Maddison 1984). As long ago as 1939, a total of 3,759 insect specimens had been taken inside propeller-driven aircraft worldwide (Whitfield 1939), and Dethier (1945) reported 11,448 insect specimens collected from aircraft in Hawaii. Mendonça and Cerqueira (1947) report 40,168 insect specimens taken on airplanes in Brazil. These studies included species of obvious medical or economic significance. The advent of jet aircraft brought an increase of an order of magnitude in the number of introduced insects in Hawaii (Beardsley 1991). Thus, potential for new introductions to the Galápagos is large. There is a serious and urgent need to institute or improve rigorous inspection and quarantine procedures at Galápagos sea ports and airports to curb the flow of new and potentially disastrous introductions.

However, quarantine and inspection alone will not completely stop insect introductions. Quarantine regulations have been applied in Hawaii since the 1890s, but introductions have accelerated in the 20th century and new pests continue to appear (Beardsley 1991); 500 have been recorded since 1965. Even with strict control, the increase in commerce with the continent and increased numbers of tour boats and ships between the islands will continue to dilute the native and endemic faunas with introductions (Silberglied 1978) and to mix the once-isolated faunas of separate islands. The erosion of the natural species compositions of all the other tropical oceanic islands worldwide should show the value of efforts to protect the Galápagos Islands, the world's last, most nearly pristine and intact, island insect ecosystem.

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