Encyclopedia of Entomology

Edited by
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University of Florida

2008

Second Edition

Volume 2
D–K

Galápagos Islands Insects: Colonization, Structure, and Evolution

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The Galápagos archipelago of Ecuador has an interesting insect fauna that is now rather well known. The archipelago is composed of 19 islands larger than 1 km^2, with a total land area of 7,882 km^2. It is the world's only remaining tropical oceanic archipelago that is little altered by humans. The present islands, 800–1,000 km west of the Pacific coast of Ecuador, have been available for terrestrial colonization for 3–4 million years. The archipelago is a model system for assessing the dynamics of biotic dispersal to, and differentiation on, oceanic islands. They are a natural experiment which has been running in oceanic near-isolation for about 3 Ma. Each island (Fig. 1) is a replicate of an experiment in biotic dispersal, colonization, and differentiation. The present plants and animals can be seen to be a record of the successes in dispersal to the islands, and of the dynamics of their subsequent evolution in isolation. The story has been well (or even exhaustively) reported for many of the larger plants and vertebrates. This story, however, has not been well studied for the vast majority of insects and other terrestrial invertebrates.

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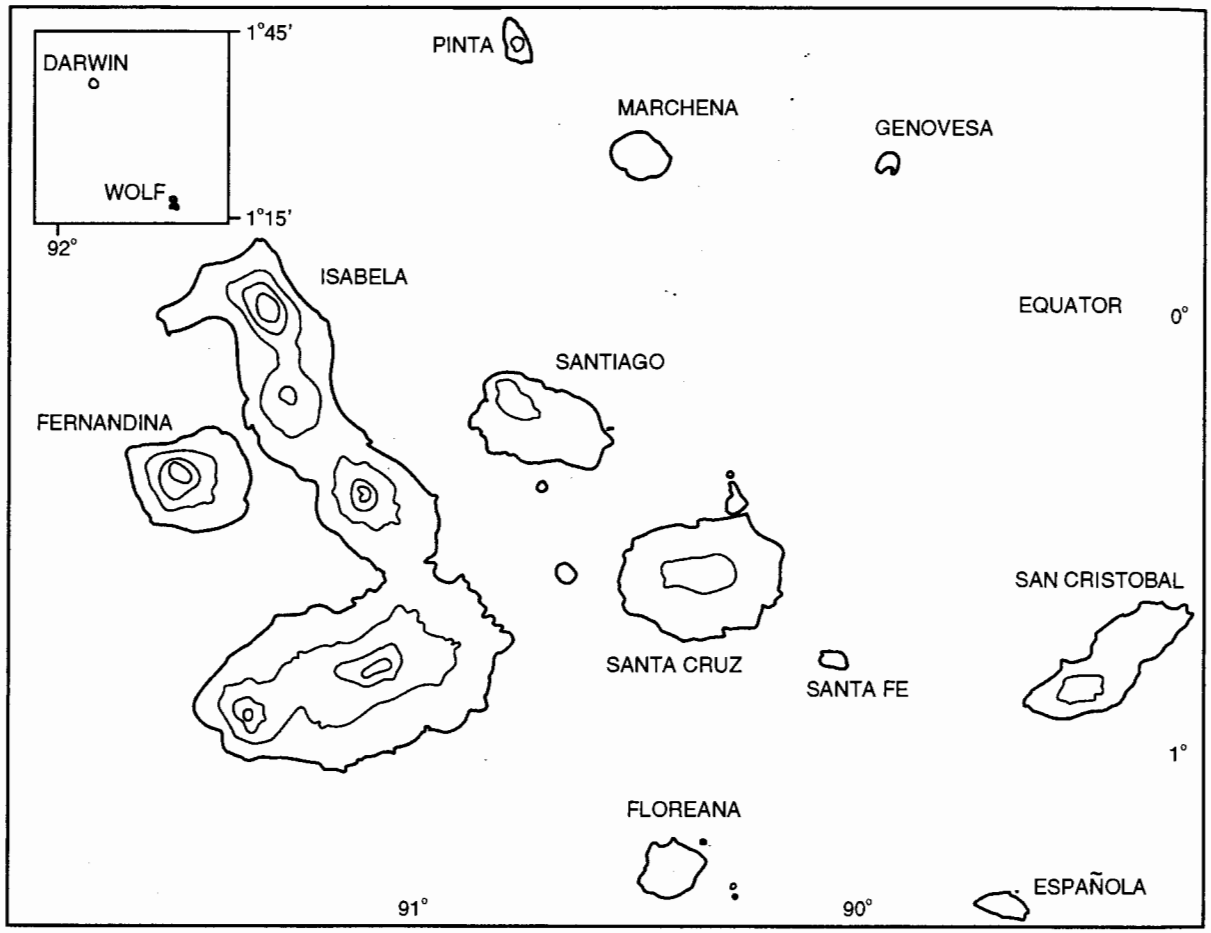


Galápagos Islands Insects: Colonization, Structure, and Evolution, Figure 1 Map of Galápagos Archipelago.

The insect fauna (Tables 1 and 2) is now known to contain 23 of the world's 31 orders of insects, with at least 255 families, 1,057 genera, and 1,853 species, of which 736+ are endemic, 818+ are indigenous, and 295+ are introduced. Within the beetles (Coleoptera), the islands have 56 families, 297 genera, and 486 species (266 endemics, 110 indigenous, and 110 introduced species). The 376 native beetle species (indigenous and endemics combined) represent a rate of species accumulation of about one every 9,260 years (through successful colonization plus speciation through about 3.5 million years).

Charles Darwin is known to have been a keen collector of insects and especially beetles. However, as he wrote in his 1845 book "Voyage of the Beagle," he was not impressed by the abundance or diversity of the insects of the Galápagos Archipelago. In fact, the entire biota of the Galápagos is generally not very impressive in appearance. But there are a few exceptions and these have received exceptional publicity. Most of the organisms are, however, small or drab when compared with those of the luxuriant tropical forests of mainland South America. This is partly a reflection of the isolation of the islands (800–1,000 km west of the coast of Ecuador), their youth (only 3–4 million years), the difficulty of dispersing to them, their seasonally harsh and semi-arid tropical climate, and the difficulty of establishment by colonizing species.

Galápagos Islands Insects: Colonization, Structure, and Evolution, Table 1 Numbers of native (endemics plus indigenous) genera, species, and single-island endemic beetle diversity, arranged by increasing island size . The larger islands have more genera, more species, more single-island endemics, and more species per genus. These generalizations also occur in the rest of the native insects fauna

Island	Area (km^2)	Total native Genera	Total native Species	Single-island species/ Endemics	Genus ratio
Caamaño	0.045	9	10	0	1.11
Beagle	0.08	1	1	0	1.0
Campeón	0.095	16	16	0	1.0
Plazas Sur	0.119	17	17	0	1.0
Eden	0.23	8	8	0	1.0
Daphne Major	0.330	3	4	0	1.33
Gardner at Floreana	0.812	7	7	0	1.0
Darwin	1.063	15	15	2	1.0
Bartolomé	1.24	16	17	0	1.06
Tortuga	1.298	3	3	0	1.0
Wolf	1.344	17	17	2	1.0
Seymour	1.838	31	33	0	1.06
Rábida	4.993	46	48	0	1.04
Genovesa	14.10	44	48	2	1.09
Pinzón	18.15	42	44	2	1.05
Santa Fé	24.13	40	48	2	1.20
Baltra	26.19	28	32	0	1.14
Pinta	59.40	76	87	0	1.15
Española	60.48	55	65	4	1.18
Marchena	129.96	56	63	2	1.13
Floreana	172.53	114	141	5	1.24
San Cristóbal	528.09	123	153	17	1.24
Santiago	584.65	119	148	14	1.24
Fernandina	642.48	72	80	1	1.11
Santa Cruz	985.55	186	258	27	1.39
Isabela	4,588.0	158	205	24	1.30

Colonization Processes

How do insects get to oceanic islands? The processes of colonization and any subsequent evolution on islands can seldom be directly observed. Usually, they are deduced from an analysis of the distributional and ecological patterns of the organisms in conjunction with evolutionary and ecological theory.

There are two general groups of hypotheses about processes which place biotas on islands. One of these, the "Continental Drift" process of distribution of ancient biotas, is irrelevant for the Galapágos because of their geological youth and oceanic origin.

Galápagos Islands Insects: Colonization, Structure, and Evolution, Table 2 Summary of numbers of species and native genera of the insect orders of the Galápagos islands. Some orders have a disproportionate number of introduced species, especially on the islands with human settlement. A figure of 1.00 in the column of native species/native genus ratios shows that there has been no speciation in many insect orders after the natural colonization event of a single species in each genus, and comparatively little in the other orders

Order	Introduced Species	Native species	Native Genera	Species/Genus Ratio
Collembola	3	35	22	1.57
Diplura	1	2	2	1.00
Archeognatha	0	1	1	1.00
Thysanura	1	2	2	1.00
Odonata	0	8	7	1.14
Orthoptera	4	29	13	2.23
Mantodea	0	1	1	1.00
Blattodea	11	7	3	2.33
Isoptera	0	4	3	1.33
Dermaptera	4	3	2	1.50
Embioptera	1	1	1	1.00
Zoraptera	0	1	1	1.00
Psocoptera	14	26	22	1.18
Thysanoptera	8	42	42?	1.00?
Hemiptera	118	198	86	2.30
Phthiraptera	8	80?	40?	2.00?
Neuroptera	0	8	5	1.6
Strepsiptera	0	1	1	1.00
Siphonaptera	3	1	1	1.00
Coleoptera	111	378	226	1.67
Lepidoptera	64	±300?	160?	1.88?
Diptera	66	±200?	150?	1.33?
Hymenoptera	46	±250?	160?	1.56?

Thus, all terrestrial colonists have crossed the oceanic water gap by one of four general dispersal mechanisms. The method of dispersal is a property of all the ecological, behavioral, and physiological characteristics of the species and of its mode and frequency of transport opportunity. Colonization is a property of both the life history requirements of the species and the characteristics of the new environment.

Aerial Transport (Actively by Flight and/or Passively by Wind)

This probably accounts for about half of the insects of the Galápagos. The mean body size of Galápagos insects appears to be smaller than for a mainland Ecuadorian fauna (but measurements are available for neither). Darwin first noted the small size of the insect fauna. The smaller body size would support

the idea that the majority of the insect colonists were carried as flying individuals by winds. In contrast to its importance for insects, it may seem surprising that wind transport may account for only 9% of natural seed-plant colonizations of the Galápagos.

Marine Transport

A significant component of the total insect fauna probably arrived on the sea surface, either on rafts of vegetation and flotsam or by floating themselves (as pleuston). This may be the most important mode for most of the flightless terrestrial arthropods. For the insects themselves, it is estimated that marine transport may also account for about half of the original colonists. Flightless or poorly flying groups of large-bodied beetles such as weevils and darkling beetles probably used this mode, as did millipedes, centipedes, terrestrial isopods, oribatid mites and others. Bostrichids, cerambycids and various other wood-boring and wood-associated beetles probably arrived by rafting in wood as adults or immatures. Flightless *Gerstaeckeria* weevils may have arrived on rafting pieces of their *Opuntia* cactus host plants.

Several groups of large-bodied wingless beetles such as endemic *Galapaganus* weevils and the three genera of Darwin's darkling beetles (genera of Tenebrionidae containing nine species that were first collected by Darwin: *Stomion*, *Ammophorus*, and *Blapstinus*) are represented by species that occur on more than one island. Such cases are usually within the older eastern and central group of islands. It is logical that these species originated (speciated) on one island and that they have then moved from this to another island, probably after being washed to sea during heavy El Niño rainstorms and floods.

Transport on or in Other Animals

Insect ectoparasites, such as all of the 80 species of Phthiraptera (chewing bird-lice) and the 8 species of Hippoboscidae (louse flies, Diptera), as well as bird ticks, reptile ticks and chigger mites, undoubtedly arrived on their vertebrate hosts. Bird transport has also been important for seed-plants, because it is estimated that 79% of the angiosperms arrived as propagules with birds, either on or in their feathers or in their digestive tracts. Rafting terrestrial mammals and reptiles seem to have carried a few arachnid and insect ectoparasites. And invertebrate colonists themselves have also carried some of their own arthropod parasites. Examples are one strepsipteran (in leafhoppers), several dryinid wasps and some pipunculid flies (in leafhoppers). Among the beetles, there are two examples: one meloid blister beetle (on *Xylocopa* carpenter bees), and two rhipiphorid beetles (in wood-boring beetle larvae) probably arrived as parasitic immatures on or in their host insects. The parasitized bee hosts themselves probably arrived by rafting on floating wood and the hosts of the rhipiphorids in lumber imported for construction of buildings.

Human Mediated Transport

Humans have intentionally introduced many domestic animals and agricultural or horticultural plants to the Galápagos. Some of these have escaped and become feral. But there is only one example of the intentional introduction of an arthropod: the vedalia beetle (Coccinellidae) for the bio-control of the cottony cushion scale (*Icerya purchasi*, Hemiptera), an introduced pest. By 1998 there were at least 292 recognized examples of unintentional introductions of insect species and the number in 2004 was at 450 species of introduced insects. Such species are here called introduced species, but the term "adventive" has also been used for these. The first such introduced insect may have arrived with the first European landings of Bishop Tomas de Berlanga and his party in 1535, as *Dermestes* (dermestid) and *Necrobia* (clerid) beetles and cockroaches. These were all commonly associated with

humans and stored products in their sailing ships. Pirates, who used the islands from shortly after the time of their discovery until the early 1700s, and whalers and sealers, from the mid 1700s to mid 1800s, may have brought an alleculid beetle (and other dry-wood insects such as bark-beetles) in logs or firewood from the mainland.

Ships transporting both supplies and tourists have taken insects attracted to ships' lights to and between the islands. The orders with the largest number of introduced species are Coleoptera, Hemiptera, Lepidoptera, and Diptera. Some 111 beetle species are among the more commonly encountered species of insects introduced to date. Not all of the introduced species seem to have become permanently established; some long-horned beetles have not been found since their original collection. The introduced species occur in greatest diversity on the four large islands with permanent human settlements. There is now a program of agricultural quarantine control and inspection of goods and materials coming into the Galápagos in an attempt to limit future introductions of alien arthropods.

Sources of the Colonists

There is limited detailed data on the mainland distributions of either indigenous Galápagos insects or mainland sister species of the endemic species. The data now available seem to indicate that only a few of the Galápagos colonist insects came from southern South America (arid coastal Peru or Chile). Most of the faunal relationships are with the lowland semi-arid and seasonal Neotropics, along the Pacific coast from Mexico to Ecuador. The best phylogenetic and biogeographic analyses show a general biogeographic pattern of a western Neotropical source area and that the Galápagos species are relatively recently derived species.

Stochastic (Random) Processes in Colonization and Distribution

Colonization is seldom strictly predictable or linear even if the islands themselves are relatively linear in age or geography. As an example, one would predict that insect colonization was first to San Cristóbal and Española, which are the oldest and most easterly islands, and that the other islands were colonized sequentially northwestward as stepping stones as they formed through time. Exceptions to these predicted patterns do exist. This shows the lack of absolute predictability in present distributions through the randomness of the processes of either past dispersal, or colonization success, or extinction. For instance, the carabid beetle genera *Platynus* and *Scarites* are on Isabela and San Cristóbal islands, and not on Santa Cruz, which lies between them. The indigenous carabid *Halocoryza acapuliana* Whitehead is known only from small and central Rabida Island.

Neighbor islands are more likely to share endemic species. This is clear in a number of shared beetle species limited to island pairs such as Darwin and Wolf (the tenebrionid *Stomion cribicollis* Van Dyke and the weevil *Galapaganus darwini* Lanteri), and Marchena and Pinta (the tenebrionid *Stomion rugosum* Van Dyke). The isolation of Genovesa is evident in its failure to be colonized by flightless *Ammophorus* beetles and other insect groups. Flightless *Galapaganus* weevils are seemingly absent from Pinta and Marchena. Pinzón is famous for not having the widespread palo santo tree (*Bursera graveolens*), but this island's insects are not well enough known to evaluate a pattern of absence of insect species there.

Randomness is evident in the fact that some colonizations have been across the archipelago (from one side of the archipelago to the other). Molecular data suggest that Pinta Island was colonized by tortoises by oceanic transport from Española, and cladistic analysis suggests the same pattern in flightless *Stomion* beetles.

Structure of the Insect Fauna

An Unbalanced Fauna

Insect representation at the family level in the Galápagos is vastly different from that in the Neotropical fauna. The cause is the inequality of families in their ability to successfully complete both the sequential processes of dispersal and then colonization. When compared to the fauna of the Neotropical continental source area, it is evident that the Galápagos fauna is unbalanced (or disharmonic) and impoverished. This means that the taxonomic composition of the archipelago is significantly different in its makeup and proportions from that of the mainland.

The probable reasons for the absence of many insect families, subfamilies, and tribes are diverse. Difficulties of long-distance over-water dispersal and colonization must lie at the core of the reasons. Long distance dispersal is unlikely for many taxa and the lack of diverse and suitable habitats in the Galápagos is of undoubted importance. The absence of suitable food plants or prey items is involved. The taxa which are present can be viewed as able dispersalists, rugged colonists, and adaptable in acceptance of available microhabitats and food materials.

Trophic Generalists

Colonization is probably easier for trophic generalists (scavengers and predators) than for herbivores which are more likely to be specialist feeders. Island insect faunas in general tend not to be as rich in herbivores as the faunas on continents. In Galápagos beetles there are more trophic generalists (scavengers and predators) than herbivores. However, in Heteropteran bugs, colonization of islands by herbivores seems to be more successful than by predators.

Trophic Specialists

There is little evidence that Galápagos insects have narrow or restricted feeding niches. The few examples are *Gerstaeckeria* weevils which feed only on the tissues of *Opuntia* cactus, and some host specific seed feeding bruchids and scolytids. *Ataenius* scarabs, usually associated with herbivorous mammal dung, feed on the dung of the herbivorous giant tortoises and land iguanas. This may or may not represent a shift to a new food type. Tortoise and land iguana dung appears similar to that of ungulates because it is mostly composed of poorly digested plant materials.

Ecological Escape

Plant or animal colonists on islands may be ecologically "released" through escape from their continental herbivores, parasites, predators, and competitors. Many cases of escape from insect herbivores or predators must exist, but few are recognized. One example is the seed-producing legume plants which have escaped many (but not all) of their seed predator bruchid beetles. The bruchid *Megacerus leucospilus* (Sharp) feeds on the seeds of the widespread beach morning-glory *Ipomoea pes-caprae* in Central America, but the plant seems not to have this seed predator on the Galápagos.

Parthenogenesis

If females of a species can reproduce without the presence of individuals of the male sex, the species is more likely to establish itself as a colonist. Several of the Galápagos insects are known to be parthenogenetic. But there is no apparent evidence that this has been disproportionately important in the colonization of the Galápagos.

Vegetational Zonation and Diversity

Terrestrial communities in the Galápagos are usually characterized according to the elevation-related (precipitation and temperature controlled)

zonation of the flora. The archipelago may possess the strongest or most compressed floristic zonation to be found anywhere in the world, passing through its six major vegetation zones in an elevational rise of only about 700 m; the littoral, arid, transition, humid forest, evergreen shrub, and above-treeline fern-sedge ("pampa") zones.

Insect diversity also seems to display some zonation, with fewer species being known from the higher elevations. The arid zone has the largest area in the islands and the most native insect species. The other zones, at higher altitudes, have progressively less area and proportionally fewer species, but sampling has not been equivalent. This probably indicates that the arid zone has been a bigger target for colonization for a longer period of time. The introduced species are more evenly distributed in all zones. This might be a reflection of the more eurytopic (adaptable) nature of the introduced species.

Plants also support diversity in that they provide various structural parts that may be fed upon by feeding specialists. Host-specific plant-feeding insects could be expected to exhibit the same zonation as their hosts, but almost all Galápagos phytophagous insects seem to feed on several species of host plant. Data for genus and family-level host-plant diversity are not available. Host specificity, to be expected in groups which elsewhere are usually monophagous or stenophagous plant-feeders, such as chrysomelids, is slight in Galápagos phytophagous beetles. There is no additional evidence for host specificity in indigenous phytophagous insects other than in *Gerstaeckeria* weevils on *Opuntia* cactus and some bruchids and scolytids. Thus, phytophagous species are in the minority, few are host specific, and none seem to have co-evolved with the endemic vegetation.

Seasonality

Environmental conditions regulate periods of insect activity. Most adult insect species are present or active during the rainy months of January to June. With the arrival of the Galápagos rainy season, insect activity increases and there are large and noteworthy outbreaks of beetles and other insects, which seem to be short-lived. These include *Calosoma* ground beetles, *Camponotus* ants, *Disclisioprocta stellata* Guenée (a geometrid moth), various sphinx moths, and other insects. These mass emergences are best noticed at lights at night and are environmentally triggered, but they also occur annually in coastal mainland Ecuador and seasonal forests elsewhere in Central and South America, so they are not a unique island feature.

Evolutionary Dynamics

Genus Level Endemism

Endemics are taxa limited to the geographic area under discussion. Genera endemic to the Galápagos probably represent an earlier time of colonization and a more prolonged period of isolation. Galápagos endemic genera are proportionally more frequent in the vertebrates and less frequent in the insects. This could mean that vertebrates differentiate at a faster rate or under stronger selective pressures, but more probably is a reflection of the more finely divided subjective criteria for what defines a vertebrate genus. Some endemic insect genera do exist. Among these endemics are some which can be called phylogenetic relicts or paleoendemics and which have no close relatives, such as the eyeless cave staphylinid *Pinostygus* of Isla Santa Cruz, and the *Neoryctes* dynastine scarabs which occur as four species on four islands. Some genera, once thought to be Galápagos endemics, have since been found in mainland Neotropical localities and others may yet be detected.

Species Level Endemism

Most insect colonization has not been followed by much species multiplication; the mean for the native beetle fauna is about 1.35 species per

colonizing ancestor. About half the naturally occurring species are endemic, depending on the insect order. These evolved to endemic status following the colonization event of the ancestral species. The factors suppressing speciation in general in the Galápagos (as compared with other archipelagos) seem to be, in probable order of importance: lack of great ecological diversity, closeness to mainland source areas, and geological youth of the islands.

Different groups of organisms need not present equivalent amounts of endemism. This is obviously a result of differences in their vagility and the amount of gene flow between continental and island populations. In beetles, the good dispersers have lower levels of endemism, while poorer dispersers have higher levels. Comparison of the Galápagos and Hawaiian archipelagos shows a much larger mean number of speciation events from a single colonist ancestor in Hawaii. This is probably the result of Hawaii's greater age, area, ecological diversity, and isolation (this is to say that colonist arrival is less frequent, and that genetic dilution of island populations by mainland genomes is also less frequent).

Speciation

Most insect genera in the Galápagos are represented by only a single species. This shows that most colonization of the islands has usually been by only one species in a genus. This pattern was first noted by Darwin. Only a minority of the native insect genera which are present contain more than one species, either through multiple colonization, or species multiplication on the islands. The process of forming several species by allopatric speciation on a single individual island has not been a dominant evolutionary process in Galápagos beetles, while it has been a spectacularly exuberant process in the Hawaiian Archipelago.

Nevertheless, there are several insect genera which have undergone appreciable subspeciation or speciation in the Galápagos but none of these approach the dramatic swarms of species (descended from a single ancestor species) of insects, snails, or birds that have evolved in Hawaii. For instance, while hundreds of species of *Drosophila* occur in Hawaii, there are only 13 species (many cosmopolitan) of in these in Galápagos.

Winged Endemic Species

In the winged insects the most common pattern of distribution is for a species to occur on more than one island. This is easy to understand. It is most likely that these evolved on a single island and then dispersed to other islands, usually by flight.

Loss of Wings

Loss of flight ability is one of the more pronounced phenomena associated with island insects. This is seemingly not a property of island life itself, but of habitat stability and homogeneity. Flightlessness also frequently occurs in insects in desert and semi-arid habitats. This last is the best single characterization of Galápagos environments, and beetles are prime examples. Flightlessness in some South African desert dwelling scarab beetles is a morphological correlate with water conservation capabilities. This may also be true and part of the adaptive strategies of such flightless Galápagos beetles as tenebrionids, carabids, and weevils. Beetle examples of more speciation in less vagile groups are in flightless carabids, weevils, and Darwin's darkling beetles (*Stomion*, *Ammophorus*, and *Blapstinus*). Interestingly, even within flightless genera in the arid lowlands, many species do occur on more than one island, and these are probably evidence of inter-island oceanic transport following the origin of the species on one island.

The single island endemics are usually restricted to either the arid lowlands or the moist uplands (of high islands). Groups that are actively in the process of losing flight ability, such as *Ataenius* and *Neoryctes* scarabs, show discrete polymorphic stages in reduction of hind wings. So, loss of flight ability in Galápagos insects is a significant

evolutionary theme. This has not always sponsored a major burst of species multiplication, but it has happened more often in groups that lost their flight ability on the Galápagos as a convergence rather than in groups that arrived already in a flightless condition. There is a parallel in birds: rails have reached many oceanic islands and then convergently experienced a reduction in wings and loss of flight ability.

Speciation and Flightlessness

Flightless terrestrial arthropods would certainly appear to have less dispersal potential than winged ones, and most species proliferation has occurred in the Galápagos beetles that are secondarily wingless. Nine genera of beetles probably colonized in a flightless condition, but only four of these have undergone island multiplication to three or more species. These groups have produced an average of 3.0 species per colonization event. Another 14 genera appear to have become flightless after colonization and these show even more species proliferation, with a mean of 3.6 species per colonization event.

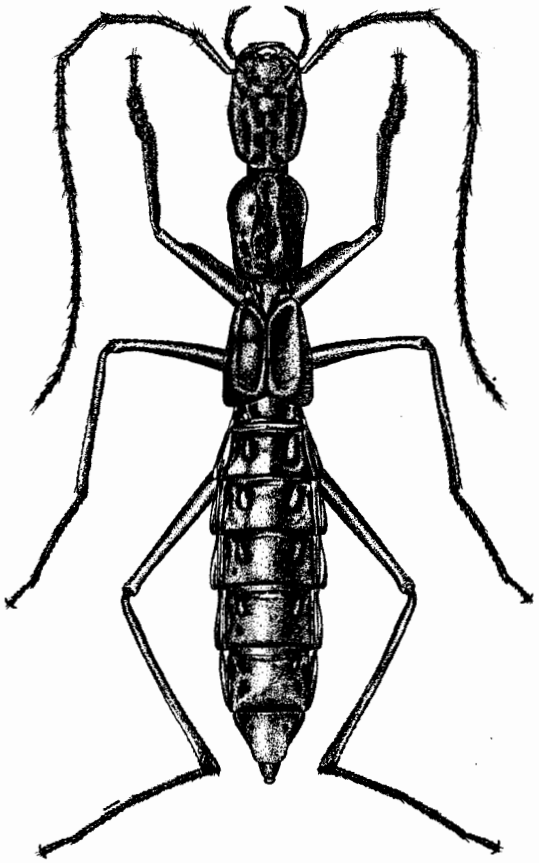
Adaptive Radiation

Adaptive radiation is a common phenomenon on islands. But it is important to note that adaptive radiation is much more than just the simple allopatric species multiplication that follows genetic isolation on separate islands. It is here defined as the set of evolutionary changes which occur in the diversification of a lineage that facilitate the exploitation of new resource types with different morphological or physiological traits. Thus, along with the morphological, physiological, and/or behavioral changes accompanying speciation must also come changes in either or both niche and habitat use. This is what has happened in the famous textbook example of Darwin's finches. Other examples can include the striking adaptive radiation in *Scalesia* trees and shrubs, and perhaps arguably in *Opuntia* cactus. In contrast, the famous giant tortoises and less famous lava lizards have undergone much speciation or subspeciation, but there is little evidence for true adaptive radiation in these examples. Adaptive radiation is probably enhanced by competition for limited resources, as in the case of the finches, especially in times of drought. But, it is difficult to envision intense competition between generalist scavenger or generalist predator insects.

Are the few examples of adaptive radiation indicative of a generalization, or are they exceptions? How many of the monophyletic species swarms in the insects of the archipelago have undergone significant ecological, morphological, or behavioral differentiation that promotes life in a new niche or new habitat? In short, there seem to be very few examples within the insects in general. In the three genera of Darwin's darkling beetles (*Ammophorus*, *Stomion*, *Blapstinus*) there are some cases of congeneric species sympatry and there is some habitat separation between species based on preferences for different substrate types (sand versus volcanic ash), habitat distance from the seacoast, and elevation. Most *Ammophorus* species inhabit the arid zone, but two are restricted to the moist highlands of San Cristóbal and Santa Cruz Islands. The same occurs in *Galapaganus* weevils. Thus, while the Galápagos are famous for having provided a classic example of the process and results of adaptive radiation in Darwin's finches, this is an exception. It is only a very infrequent or arguable result in Galápagos insects.

Subterranean Arthropods

A diverse assemblage of many eyeless arthropods occurs in the extensive systems of caves and rock crevices in the volcanic basalt bedrock of the Galápagos. Some ten species of arthropods such as geophilomorph centipedes, polydesmoid millipedes, soil dwelling earwigs, and darkling and carabid beetles are in eyeless (Fig. 2) genera which must have colonized the Archipelago in an already-eyeless condition. But at least another 23 species of



Galápagos Islands Insects: Colonization, Structure, and Evolution, Figure 2 The staphylinid beetle *Pinostygus galapagoensis* Campbell and Peck from a lava tube cave on Santa Cruz island. This eyeless and flightless subterranean endemic genus and species has probably changed more from its ancestral colonizing species than any other Galápagos animal. The beetle belongs to a group of visually hunting and flying arboreal predators which live in the canopy of tropical South American rainforests. No other members of its tribe occur in the Galápagos. The body length is about 2.5 cm, and this is the world's largest eyeless-wingless staphylinid beetle.

eyeless terrestrial arthropods, including seven beetle genera, are in normally eyed groups. These must have lost their eyes after colonizing the islands, and during the process of adapting to soil, litter or subterranean habitats.

Extinction

Extinction through time is a natural process and is to be expected. But extinction caused by human action is different and should be of great concern in the Galápagos. Insect species extinction through human causes is probable, but no documented individual examples are known. Some of the introduced insects, such as *Wasmannia* fire ants and *Polistes* wasps, are preying on or competing with indigenous and endemic insects.

Feral vertebrates have had a two-fold effect on beetles and other insects. (i) The vertebrates have caused the near or complete loss of insect host plants, such as *Opuntia* cactus on most of Floreana and San Cristóbal (eaten by feral goats and donkeys). This has led to the concomitant loss of host-specific insects such as *Gerstaeckaria* weevils. (ii) The vertebrates have also had an effect by being predators, such as mice or rats or pigs, feeding on *Neoryctes* scarab beetles or other large-bodied insects. Despite these examples, there is presently no strong or direct evidence of the actual archipelago-wide extinction of an insect species on the Galápagos through an action ultimately caused by human activity.

Human-caused habitat alteration has had a significant, but unmeasured effect on the native insect populations. The clearing of large areas of *Scalesia* forest for agriculture and pastures and the replacement of large areas of native vegetation by introduced crop plants, grasses and weeds on Floreana, Santa Cruz, San Cristóbal, and Isabela must have had some impact. The importance of all of these introductions and alterations has not been measured or even estimated for the beetles or other insects.

Future Research

Although much is now known about Galápagos insects, there is still much to learn, especially about the life histories and evolutionary relationships of the species and in comparing them with the continental South American insect fauna. The Galápagos National Park Service and Charles Darwin Research

Station invite international research proposals and scientific collaboration with Ecuadorian personnel, students, and researchers. Information on past and present entomology research programs and details for scientific research permit applications can be found at http://www.darwinfoundation.org/terrest/entomology.html. Research proposals of an applied and conservation orientation are especially welcome. General collecting without a research purpose is not permitted.

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