costs. They were higher than in all previous El Niño years.

Whatever the reasons, patterns of breeding on Daphne are not unique, but are likely to occur in parallel fashion elsewhere on other islands when effects of El Niño conditions are experienced throughout the archipelago. In previous El Niño years, Darwin’s finches on two widely separated islands, Genovesa (Grant and Grant 1989) and Daphne Major (Gibbs and Grant 1987), responded in the same way to heavy rain and a prolonged wet season (Grant and Grant 1996). Clutch sizes were elevated and finches bred repeatedly. In 1998, short-term observations of ground finches on other islands indicated repeated breeding, but an early cessation, perhaps even earlier than on Daphne (D. Day, M. Hau, and M. Wikelski, pers. comm.).

One of the things we have learned from this long-term study is that no two El Niño years are alike. An obvious reason for this is the amount of rain and the number of months in which it falls varies among El Niño years. However, this is not the only reason. Responses to El Niño conditions are determined in part by preceding conditions, be they dry or wet, food-rich or food-poor. Those preceding conditions in turn are determined by whether drought or normal conditions precede the Niño perturbation and on the interval since the previous Niño event. For example, finch population densities were much higher at the beginning of 1998 than at the beginning of 1983, and finches probably interfered with each other’s attempt to breed at the beginning of 1998. This, we believe, is one reason why finch breeding took so long to get underway in 1998. Thus, effects of El Niño can be fully understood only by placing them in their temporal context. We would never have learned this lesson if the Niño watering experiment had been under our control.

ACKNOWLEDGMENTS

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EL NIÑO AND INTRODUCED INSECTS IN THE GALÁPAGOS ISLANDS: DIFFERENT DISPERAL STRATEGIES, SIMILAR EFFECTS

Lázaro Roque-Albelo and Charlotte Causton

INTRODUCTION

Oceanic islands are considered fragile ecosystems. The introduction of one or more alien species can often lead to a series of important ecological alterations. Alien species are often able to rapidly colonize oceanic islands in the absence of natural enemies and other biotic factors that, in their native range, maintain population numbers at a natural level. These species often possess characteristics that enable them to occupy a wide variety of niches that have yet to be filled by native species and, in some cases, can displace them (Vitousek 1998).

A 960-km oceanic barrier has isolated the Galápagos Islands from continental America, but recent colonization by humans has increased the introduction of alien species to the islands. Peck et al. (1998) have identified 292 introduced insects from the Galápagos Archipelago and it is estimated that there are many more to be found. Accidental transport by humans is the principal cause for these introductions, while a variety of methods is responsible for the distribution of these insects within the Archipelago, including dispersal by air currents. It has long been suspected that the periodic El Niño events contribute to insect dispersal to and within the Archipelago. However, to our knowledge, published information about the impact of these irregular climatic conditions on the behavior and dispersal strategies of alien insects is non-existent.

Six alien insect species are highly aggressive and a threat to the flora and fauna of the Galápagos Islands. In 1997, the Entomology Program of the Charles
Darwin Research Station was amplified and a concentrated effort made to find funds to monitor the population numbers and distribution of three of these aliens: the cottony cushion scale, Icerya purchasi Maskell, and two wasp species, Polistes versicolor Olivier and Brachygastra lechuguana Fabricius. Although funding has not been secured for the remaining three species (two fire ant species, Wasmannia auropunctata Roger and Solenopsis geminata (Fabricius), and the biting black fly, Simulium bipunctatum Malloch), surveys within the Archipelago have permitted us to make observations about the distribution and behavior of these species.

In this article, we present a summary of observations of the behavior of these species during the El Niño event of 1997-98, including new distribution records.

**LITTLE FIRE ANT**

The little fire ant, Wasmannia auropunctata Roger (Figure 1), is probably the most aggressive species that has been introduced into the Archipelago. Lubin (1984) and Clark et al. (1982) observed a marked reduction of scorpions, spiders, and native ant species in areas infested by the little fire ant. Many other arthropods are probably also affected, but this has not been measured.

Arriving in the Archipelago between 1910 and 1920 (Kastdalen 1964), it first colonized Santa Cruz. Since then, it has become established on San Cristóbal, Isabela, Floreana, Santiago (Silberglied 1972), Santa Fe (de Vries 1975), Pinzón, and Marchena (Abedrabbo 1992). The ants were most likely transported between the large islands on plants and in soil, and the small islands by camping provisions and equipment. *W. auropunctata* is atypical of many ant species in that it does not rely on the winged queen to form a new colony. Instead, it forms a network of satellite colonies connected by a complicated tunnel system under rocks, soil, and decomposing leaf litter. Each satellite colony contains several queens and numerous workers and immatures at various stages of development. Over time the colony radiates outwards from its center of origin and comes to occupy extensive areas.

The likelihood of eliminating the little fire ant from the Archipelago without seriously affecting the indigenous (native and endemic) invertebrate fauna is low, most notably on the larger islands where the little fire ant is now distributed over hundreds of hectares. Control of the little fire ant has hitherto been by non-selective ant poisons, fire, or by clearing vegetation. Eradication programs are expected to be more successful on the smaller islands or in isolated areas where distributions are less than a few dozen hectares. *Wasmannia auropunctata* has been successfully eradicated from Santa Fe (Abedrabbo 1994) and it is hoped that funds will be secured to initiate eradication programs on the other smaller islands, such as Marchena.

During the atypical “garúa” or dry season (May-December) of the El Niño event of 1997-98, little fire ant populations on Santa Cruz increased notably. Pit fall traps and litter samples sifted through Winkler sieves in our permanent monitoring plots in the humid zone of Santa Cruz (Los Gemelos, Scalesia pedunculata forest) were dominated by *W. auropunctata*. However, the most notable change in population numbers was observed on Marchena, where a census in August 1998 revealed that the little fire ant distribution had increased from 2 ha in 1996 (Garcia 1996) to 18 ha...
This alarming increase may be associated with the high precipitation rates and other factors related to El Niño, or perhaps to the incomplete census methodology applied in previous years.

**TROPICAL FIRE ANT**

*Solenopsis geminata* (Fabricius), the tropical fire ant (Figure 2), was also introduced at the turn of the century (Wheeler 1919) and has now colonized the islands of Santa Cruz, Floreana, Isabela, and San Cristóbal. *S. geminata* is a voracious feeder on invertebrates and may have an impact on the nesting behavior of land iguanas and tortoises (Williams and Whelan 1991, Tapia 1997). Fire ant colonies are localized on the soil surface and in leaf litter. New colonies are founded by winged females capable of flying over large distances. This dispersal tactic results in scattered colonies, which hinders control.

In 1998, *S. geminata* was recorded for the first time from the Marielas Islets, off the west coast of Isabela. These islets are nesting sites of one of the highest concentrations of penguins (*Spheniscus mendiculus Sundevall*) in the Archipelago (Mills and Vargas 1997) and there is concern that the fire ants may have an impact on nesting behavior and penguin young. Fire ant infestation on this islet was so high during our collecting trip that some activities needed to be cancelled. *S. geminata* was the only species of ant collected from 40 bait traps that were placed on the larger of the two islets. Some black rats trapped overnight in Tomahawk live traps during the same survey were found dead and surrounded by ants that were likely responsible for the mortality (H. Snell and H. Snell, pers. comm.). The presence of this ant species was not reported in surveys prior to this trip (H. Snell and H. Vargas, pers. comm.), suggesting that this species may have arrived during the El Niño event, with population numbers expanding under favorable conditions. Likely dispersal centers for the tropical fire ant are the urban areas, agricultural areas, and the volcanoes of southern Isabela, Cerro Azul and Sierra Negra.

**WASPS**

Two species of paper wasp have been introduced into the Archipelago in recent years: *Polistes versicolor* Olivier and *Brachygastra lecheguana* Fabricius (Vespidae). Contrary to some reports (G. Onore, pers. comm.), *B. lecheguana* (Figure 3) is highly aggressive in the Galápagos Islands and produces a painful sting in humans. Both species are voracious predators of larva of Lepidoptera and, on a lesser scale, other insects, which are important food sources for reptiles and birds. The impacts that *P. versicolor* (Figure 4) has on insular ecosystems are discussed by Abedrabbo (1991) and Heraty and Abedrabbo (1992).

*Polistes versicolor* was first detected in Floreana in 1988 and is thought to have been introduced in a shipment of bananas (Abedrabbo 1991). Since then, it has been found throughout the Archipelago. *B. lecheguana*, on the other hand, was reported from Santa Cruz in 1994 and, for the first time, in San Cristóbal in 1998 (D. Bonilla, pers. comm.). The dispersal strategies of these species are principally by active flight or on tourist, fishing, and cargo ships that constantly navigate the Archipelago. Nest formation in *P. versicolor* requires a single gravid female, while nests of *B. lecheguana* are founded by numerous individuals. The fundamental differences in the processes used to form the nests and in wasp nest size and structure may account for the presently limited distribution of *B. lecheguana*.

During the months of heavy rainfall from December 1997 to May 1998, population numbers of both these species diminished. Low numbers were recorded at the commencement of a monitoring program in June 1998, with numbers increasing once the dry season set in. Large numbers of *Polistes versicolor* are observed every dry season, particularly in the coastal areas, and both species are reported to be more aggressive during this period.

**BLACK FLY**

*Simulium bipunctatum* Malloch (Figure 5) belongs to the family Simuliidae, members of which include vectors of river blindness (onchocerciasis) and *Leucocytozoon*, a parasite of white blood cells in birds. *S. bipunctatum* is recorded from Central and South America and the Caribbean and is found in the coastal regions of Ecuador in the Province of Esmeraldas (Shelley *et al.* 1997). The females feed on vertebrate blood and in many countries are considered serious pests.

Although this fly is known to be largely zoophilic (Shelley *et al.* 1997), in Galápagos it is anthropophilic (feeding on humans), causing large painful welts and intense itching. In the rainy season, swarms of these small flies impede farmers from working on the island of San Cristóbal and have been the cause of some farmers abandoning their homesteads. Fly larvae develop in
fresh, flowing water and feed on protozoans, algae, and other single-celled organisms and particulates suspended in the water. The impact that this species has on native fauna is unknown. A survey by Gerecke et al. (1995) found that the sessile larvae covered all substrates in the streams of San Cristóbal, which may cause the displacement of native freshwater invertebrates.

Commonly known as the “mosca chupa sangre” or “carmelita,” this biting fly was first discovered on the island of San Cristóbal in 1989 (Abedrabbo 1992, Abedrabbo et al. 1993). Reports suggest that adults were accidentally introduced in a shipment of bananas from mainland Ecuador.

Adult females have a high dispersal capacity and some Simulium species are able to fly more than 100 km in search of a food source. In the years preceding the 1997-98 El Niño, the biting fly was only established on San Cristóbal and was mainly limited to the highland regions (higher than 300 m above sea level) of La Toma. This is the only permanent source of running water on the island and restricts the distribution of this fly. High rainfall and unusual weather conditions during 1997-98 enabled this biting fly to spread to lower elevations, as well as to other islands where freshwater sources were found. In 1997, the fly was recorded for the first time in temporary streams in Santiago (Los Aguacates) (W. Tapia, pers. comm.). We also collected it from Floreana (Asilo de la Paz) in May 1998 and from Darwin Volcano (Isabela) in February 1999. The absence of the fly in collections during the dry season of 1998 in the first two islands suggests that the biting fly was not able to establish permanent populations.

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Figure 5. Simulium bipunctatum.
Drawing by Christine Parent.

COTTONY CUSHION SCALE

Native to Australia, the cottony cushion scale, Icerya purchasi Maskell (Figure 6), has reached 80 countries, where it is known to attack more than 200 plant species (Hale 1970). Females of I. purchasi are hermaphrodites and colonies are rapidly established. The cottony cushion scale attaches itself to plants, inserts its sucking mouth parts into the plant, and extracts liquid nutrients that are essential for the plant. Heavy infestations of the cottony cushion scale cause leaf abnormalities and can cause leaf drop. This species is known to transmit plant diseases which can lead to plant mortality.

The cottony cushion scale was first discovered in the Galápagos Archipelago in 1982 and is thought to have been introduced in a shipment of Acacia trees. Since its introduction, the cottony cushion scale has invaded at least nine islands of the Galápagos Archipelago. Most introductions are likely to be associated with the transport of agricultural produce between islands. However, the cottony cushion scale may have been carried to some islands by wind currents.

In 1998, a research program was initiated to study the ecology of the cottony cushion scale and its natural enemies, evaluate its impact on native plant species and determine its distribution within the Archipelago. Since the project was started, the number of plant species for which I. purchasi infestations have been recorded has increased from 22 to 44 species: 15 endemic plant species, 23 native species, and 6 introduced species (including citrus trees) in the Galápagos Islands. Reports suggest that leguminous species are most commonly infested, with the heaviest damage on Acacia spp., Parkinsonia aculeata, and seedlings of Piscidia carthagenensis (matazarno). The white mangrove, Laguncularia racemosa, is also highly susceptible to scale attack. Plant deaths have been recorded in eight species, two of which are endemic to the Islands: Acacia rorudiana and the endangered Calandrinia galapagos. The cottony cushion scale is considered a serious threat to the native flora of the Galápagos, as well as to citrus production.

Immature stages of scale insects are commonly dispersed by wind. Studies of a closely related species, Icerya seychellensis, in the Seychelles Islands (Hill 1980) indicated that wind currents were primarily responsible for its rapid establishment on all islands within the main archipelago within a six-year period. During the 1997-98 El Niño event, I. purchasi was found for the first time on Pinzón (July 1998) and Marchena (August 1998). Warm air currents during the Niño year may have facilitated the dissemination of the cottony cushion scale to these uninhabited and less frequented islands.
Low population numbers of *I. purchasi* were observed during the months of high rainfall (December 1997-May 1998). Raw data collected from a long-term monitoring program (initiated in June 1998) on four plant species on Santa Cruz recorded zero or very low scale numbers per branch in June-July 1998, at the onset of the dry season. Since then, numbers have increased progressively. To our knowledge, the population biology of *I. purchasi* has been poorly studied in countries with only two distinct seasons. In temperate countries, maximum numbers of *I. purchasi* in California (Quezada 1969) and in South Australia (Prasad 1992) were collected during the hottest months. Heavy infestations of a closely related species, *I. aegyptiaca*, in Pacific atolls are associated with prolonged dry weather (Waterhouse 1991). There is some concern that, if the predicted drought conditions follow El Niño, a population explosion of *I. purchasi* will occur.

**DISCUSSION**

During El Niño events, the moderate south-south-east winds that are generally prevalent in the Galápagos (May-December) are converted into strong east winds. Peck (1994) suggested that the winds in a strong El Niño year create favorable circumstances for the transport of insects between islands and from South and Central America to Galápagos. Our observations show that the distribution of some introduced species expanded during the 1997-98 El Niño event. Air currents (immature stages of scale insects), active flight (wasps, black fly, and tropical fire ant), colony budding (little fire ant), and accidental transport by humans are the suggested modes of transport between islands during this period (Table 1).

The islands that are most affected by insect incursions in the Galápagos Archipelago are the central, inhabited islands. The dates of colonization on each island of *I. purchasi, P. versicolor, S. geminata*, and *S. bipunctatum* suggest that the direction of colonization in the islands is from southeast to northwest. These species are all able to disperse by wind currents and these suggest that other species that use the same dispersal strategies will show similar patterns. A detailed analysis of the colonization processes by introduced species will provide us with a better understanding of pest incursions in the Galápagos. If this hypothesis is valid, the most pristine islands with high habitat diversity, such as Fernandina and Pinta, run the risk of receiving introduced species from the central islands. Favorable climate conditions during El Niño events may accelerate these dispersal processes.

El Niño events are associated with high levels of precipitation and strong winds. In 1997-98, the total annual rainfall was up to eight times higher than in the previous years (CDRS meteorological reports). These climatic conditions favored species that tolerate wet conditions, such as the fire ants and the black fly. On the other hand, numbers of precipitation-intolerant species such as the cottony cushion scale and the wasps declined. However, the impact of a strong El Niño event is not over with the termination of the rains. These events are often followed by extended drought periods (La Niña), which, in turn, favor drought-tolerant species such as the cottony cushion scale. Numbers of these aggressive species rapidly recuperate, often resulting in population explosions.

High levels of rainfall in the arid and transition zones and, to some extent, in the higher humid zone were associated with an increase in vegetation growth (Aldaz and Tye, this volume), with the expected result of an increase in phytophagous insects and decomposers. Prey availability for predators such as the fire ants was abundant and may have been very significant in stimulating the spread of the little fire ant and the tropical fire ant. High precipitation rates also produced many temporary streams that were rapidly colonized by the black fly. Population explosions and expansion increased the probability of transport to other islands. The consequences of the aggressive species colonizing new habitats has a heavy impact on native fauna through competition for niches and by predation.

Although these “abnormal” climatic conditions increased the range of some species within the Archipelago, it should be pointed out that El Niño is a natural, cyclical phenomenon that is not directly responsible for the decline in biological diversity. As in other tropical islands, the erosion of biological diversity is a result of accelerated human migrations introducing new species (Boardsley 1991), a problem exacerbated in Galápagos by the absence of an inspection and quaran-
Table 1. Dispersal patterns and distribution of six introduced species in the Galápagos Archipelago.

<table>
<thead>
<tr>
<th>Species</th>
<th>Origin</th>
<th>Range</th>
<th>First recorded in Galápagos</th>
<th>Distribution (* = new record)</th>
<th>Means of dispersal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wasmannia auropunctata</td>
<td>Neotropical</td>
<td>Cosmopolitan</td>
<td>1910-1920</td>
<td>Floreana, Isabela, Marchena, Pinzón, Santiago, San Cristóbal, Santa Cruz, Santa Fe</td>
<td>Soil and plants</td>
</tr>
<tr>
<td>Solenopsis geminata</td>
<td>North, Central and South America</td>
<td>Cosmopolitan</td>
<td>1919</td>
<td>Floreana, Isabela, San Cristóbal, Santa Cruz</td>
<td>Soil, plants, and active flight</td>
</tr>
<tr>
<td>Polistes versicolor</td>
<td>Neotropical</td>
<td>Neotropical</td>
<td>1988</td>
<td>All major islands</td>
<td>Air currents and active flight</td>
</tr>
<tr>
<td>Brachygastra lecheguana</td>
<td>Neotropical</td>
<td>Neotropical</td>
<td>1994</td>
<td>San Cristóbal, Santa Cruz*</td>
<td>Air currents and active flight</td>
</tr>
<tr>
<td>Simulium bipunctatum</td>
<td>Neotropical</td>
<td>Neotropical</td>
<td>1989</td>
<td>San Cristóbal, Floreana*, Isabela*, Santiago*</td>
<td>Air currents and active flight</td>
</tr>
<tr>
<td>Icerya purchasi</td>
<td>Australia</td>
<td>Cosmopolitan</td>
<td>1982</td>
<td>Baltra, Floreana, Isabela, Marchena*, North Seymour, Pinzón*, Santiago, San Cristóbal, Santa Cruz</td>
<td>Air currents, and plants</td>
</tr>
</tbody>
</table>

In a more positive tone, Galápagos is now the most pristine archipelago in the world and still possesses 96% of its original fauna and flora. However, time is running out.

CONCLUSIONS

Prevention is better than cure!

Peck et al. (1998) demonstrated that insect incursions are strongly correlated with human migrations to the islands and points out that most have occurred in the last twenty years. What can we do to put a halt to this influx of new species and conserve the biodiversity of Galápagos? The installation of an inspection and quarantine system both in the Archipelago and on the continent is urgently required, in addition to complementary projects, such as decreasing the dependence on imported products by increasing local agricultural production, an ecological monitoring system to detect new incursions, and an intensive educational campaign aimed at the islanders. Some funding has been acquired to initiate some of these activities, but long-term funding is essential if we are to maintain these programs. Funding is also urgently required to develop control programs for the aggressive introduced insects such as the biting fly and the little fire ant.

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