

An illustration in black ink on a red background. It depicts two penguins on the left, perched on a rock. One penguin is facing forward, while the other is slightly behind it. To the right, an iguana is perched on the same rock, facing the penguins. The iguana's long tail extends downwards. The artist's signature 'Wedi Snell' is visible near the iguana's front leg.

# NOTICIAS de Galápagos

No. 60 December 1999







# Noticias de Galápagos

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No. 60

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## THE ORCA IN GALÁPAGOS: 135 SIGHTINGS

Godfrey Merlen

### INTRODUCTION

The toothed cetacean, *Orcinus orca*, known commonly as the killer whale or orca, occupies an ecological role as top predator throughout its world-wide range. From verbal reports, it has been known for a long time that they are regular visitors, if unpredictable as to location, to the Galápagos Archipelago, but no concentrated effort has been made to identify their range, prey, or identity.

As a consequence, there is little information concerning the effect orcas may have on the marine ecosystem of Galápagos, on the behavior of their prey species, or even their distribution both temporally and spatially. This was mainly because of the small number of vessels navigating the waters, the lack of record-keeping, and the large size of the Archipelago. Nevertheless, over the last 50 years, some records are available that reveal the presence and, occasionally, the feeding activities of these social marine mammals. During the last 10 years, many more vessels, especially in the tourist trade, have been navigating the waters of the Archipelago. This has been particularly so within the

Archipelago, rather than in the seas outside it. The increasing number of observations from these boats have been complemented by several scientific expeditions that provide records outside the Archipelago during part of the same time span. Since 1992, advantage has been taken of the increased number of people traveling through the Archipelago by introducing a more regular marine mammal monitoring program using standardized sighting sheets. I have accumulated 135 sightings, some with observations on behavior and prey, which may allow at least some generalizations to be made about orca life in Galápagos.

Of all cetaceans, the orca is perhaps the best known and the most distinctive. This makes them a suitable subject for a survey, such as the one in this report, since their clear black-and-white markings, their lack of fear of boats, the remarkable development of the adult male dorsal fin, and the fact that their feeding activity attracts large seabirds, such as frigatebirds, *Fregata* spp., all help to locate, identify, and approach orcas. At a distance, females, young males, and calves could be confused with false killer whales, *Pseudorca crassidens*, and perhaps pilot whales, *Globicephala* spp., but a close-



Social animals, an orca family swims off Punta Espejo, Marchena Island, December 12, 1991.

Photo by Godfrey Merlen.



er view, which is often easy to obtain, when the black-and-white markings become visible, eliminates any doubt.

## METHODS

The sources of the sightings include:

1. Personal sightings within and outside the Archipelago whilst undertaking marine mammal searches.
2. Library search at the Charles Darwin Research Station.
3. Sighting sheets (a slightly modified NOAA marine mammal sighting form). These were filled out by National Park-trained tour guides (who receive some guidance on marine mammal identification in their training course), who work on every vessel licensed to operate in the Galápagos tourist trade. Forms were also returned by other individuals such as boat captains, film makers, scientists, and yachtsmen.
4. Records from scientific expeditions which have been studying cetaceans.
5. Records compiled after personal conversations with witnesses.

## BIAS

Although there have been attempts to maintain sighting lists of cetaceans in the past, they have generally been included in general observation programs and as such not specific to cetaceans. Only in the last four years has a more concentrated system been operating. Thus many more sightings appear in recent years, which does not necessarily indicate an increase in the number of orcas or the frequency of their occurrence in Galápagos waters. An additional source of bias is generated, because most tour boats travel by night and visit specific land areas during the day. Thus most of the sightings by tour guides are from limited areas near the shoreline. However, because orcas feed on sea lions and many of the visitor sites are near sea lion colonies, the chances of seeing passing orcas is probably enhanced, since orcas may come close to the shore specifically to feed in these areas. Luckily, boats traveling in deep water, supplying offshore sightings, may tend to balance this near-shore bias and give a better overall view of orca activity in the Archipelago.

## RESULTS

For the analysis of the data, the inshore was defined as all waters less than 1000 m deep, while the offshore waters were considered to be those greater than 1000 m deep.

## Composition of the pod

Appendix 1 lists the sightings in chronological order. The average size of the pods was 3.11 animals ( $n = 134$ ), or 3.46 if the exceptional sighting of 48 animals (June 15, 1981) is included. The range of the sightings was between a pod size of one (32.6% of the sightings) and 48 (0.75%) (see Figure 1). However, if the pods were separated into "offshore" and "inshore," then a rather different composition was apparent. The pods offshore contained 5.08 animals ( $n = 49$ ) whilst those inshore contained 1.98 ( $n = 86$ ). The small size of the 86 inshore pods was influenced by the fact that 40 sightings (46.5%) were of single animals, of which 13 were identified as mature males.

Amongst the total of 135 pods, 57 pods have some identification as to age or sex, *i.e.*, male, female, calf. Mature males were identified in 49 of them (83%).

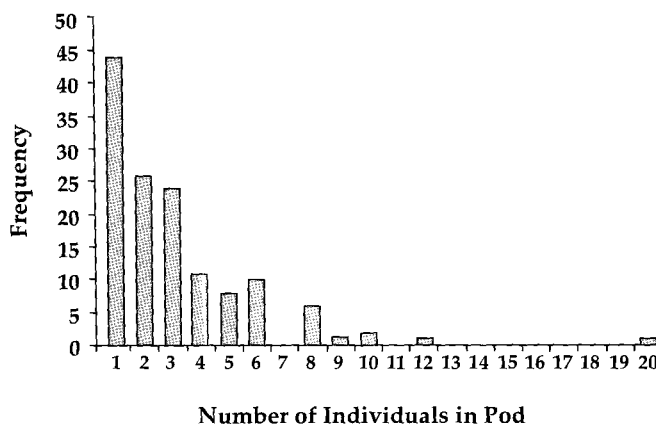


Figure 1. Range of pod sizes and their frequency of occurrence. This chart excludes the exceptional sighting of 48 orcas on June 15, 1981.

## Prey items

Orcas in Galápagos appear to be carnivorous generalists (Table 1). Although there is sometimes no direct evidence that an animal has been killed by orcas, for this often appears to occur under water, the proximity of orcas to freshly killed animals, sometimes displaying raking teeth marks or pools of blood, implicates them in an attack.

Although there are few witnesses to sea lions being killed by orcas, it is perhaps significant that 45 of all sightings (40%) are close to large sea lion colonies, *e.g.*, Plazas (Santa Cruz), Gardner Bay (Española), Punta Cormorán (Floreana), Puerto Egas (Santiago), and the Canal de Bolívar between Fernandina and Isabela islands.



**Table 1.** Species attacked or harassed (no evidence of physical contact made).

Species	Bitten/Killed	Harassed
Shark - Carcharhinidae	1	0
Hammerhead shark, <i>Sphryna</i> sp.	1	0
Manta ray, <i>Manta hamiltoni</i>	5	0
Sting ray, <i>Dasyatis</i> sp.	1	0
Sunfish, <i>Mola mola</i>	0	1
Snapper, <i>Lutjanus</i> sp.	0	1
Green turtle, <i>Chelonia mydas</i>	1	0
Fur seal, <i>Arctocephalus galapagoensis</i>	1	0
Sea lion, <i>Zalophus californianus</i>	2	1
Sperm whale, <i>Physeter macrocephalus</i>	2	1
Cuvier's beaked whale, <i>Ziphius cavirostris</i>	2	0
Bottle nosed dolphin, <i>Tursiops truncatus</i>	1	0
Common dolphin, <i>Delphinus delphis</i>	1	3
Rorqual - Balaenopteridae	1	1
Pilot whale, <i>Globicephala macrorhynchus</i>	0	1

## DISCUSSION

Orcas have been sighted near virtually every island in the Galápagos Archipelago (Figure 2) and are present in the region in all months of the year. For example, in the east and northeast of Santa Cruz, there are 21 reports spread over every month of the year, with maximums of 3 in March and 3 in August. Not only do they travel close to the shoreline, but they also, at least occasionally, swim into very shallow water (< 4 m) and enclosed bays, apparently in search of food. At the same time, they are not uncommon in the deep waters (2000-3000 m) off the edge of the basaltic Galápagos Platform (400 m average depth), from which many of the islands were volcanically built. The pods appear to travel continuously, as there are no reports of orcas remaining in any location for days, or even more than a few hours at a time.

An unanswered question is whether orca pods are resident within the Archipelago or whether they are oceanic wanderers who visit the islands from time to time on an irregular or regular basis.

Pod size is variable, with an average of 3.11 with larger pods (average 5.08) being found offshore. It is rare, apparently, to find pods of over 10 animals. Lone animals are common, especially near shore, where they compose 50% of the sightings. Since orcas are social animals, I suspect that some of the lone animals belong to larger pods whose other members are perhaps acoustically in touch, but not seen by the observer. From the 26-year study of orcas in British Columbia (Ford, Ellis, and Balcomb, 1994), "resident pods" typically contain between 10 and 20 individuals and are highly structured socially. The off-shore transient pods are smaller in size, less vocal, and may consist of a lone male. Thus, in that respect, the orcas of Galápagos seem to resemble the transients of North America.

They also resemble them in being predators on marine mammals rather than fishes. Very few underwater recordings are available from the orcas in Galápagos, but one that was made off the south coast of Fernandina on June 17, 1994, may contain elements that resemble those of the transients of British Columbia (Dr. John Ford, pers. comm.).

Dr. Mike Bigg at the Biological Research Station in British Columbia was the first to recognize that it was possible to identify orcas from the shapes of their fins, which differ through genetic characteristics or through damage, and the shape and intensity of the gray saddle markings behind the dorsal fins. These differences can be recorded photographically (Bigg, Ellis, and Balcomb 1986). From this technique, it has been possible to study family relationships and movements of pods. At present, an attempt is being made to photograph local animals in Galápagos, as this may be the only way to settle the question of whether the orcas of Galápagos are transients or residents and, if transients, whether the same individuals return.

Several sightings reveal insights into orca behavior.

Sighting 41. In 1985, an orca half beached itself on the steep shoreline of rounded boulders on the north shore of South Plaza Island in an attempt to catch sea lion pups (National Park Guide Richard Polatty, pers. comm.). This type of behavior is well known in orcas from Argentina and the Crozet Islands (David Parer, film-maker of "Wolves of the Sea," pers. comm.).

Sightings 52 and 54. On March 7 and April 5, 1991, Dr. Hal Whitehead reported that sperm whales, *Physeter macrocephalus*, chased orcas. In the first case, 12 sperm whales pursued 3 orcas (1m, 2f.). In the second about 20 sperm whales chased 8 orcas (1m., 5f., 2c.) for about 5 minutes.

Breaching has only been recorded twice (sightings 16 and 101). In one pod, followed by the author for four hours on June 17, 1994 (sighting 78), spyhopping occurred 5 times and inverted tail lobbing 6 times. Spyhopping also occurred once in sighting 121.

Common dolphins appear to be an accessible prey of orcas (n = 3. Sightings 48, 93, 105). This might explain the highly-strung and suspicious nature of these small cetaceans in the waters of the Archipelago. Perhaps they are an important prey item of orcas. Orca hunting strategy appears to be to follow fleeing dolphins and to single out a lone animal from the often large dolphin schools (30-1000 individuals), perhaps a straggler which then seems to fall as easy prey.

When orcas approach sperm whales, it seems that the sperm whales cease to make sounds (sightings 47 and 125). We found that pilot whales in close proximity to orcas (sighting 121) behaved totally differently, making an enormous barrage of whistles. We could only suppose that their ultimate defense was to try to confuse the sonar of the orcas, which was occasionally audible through the whistles.



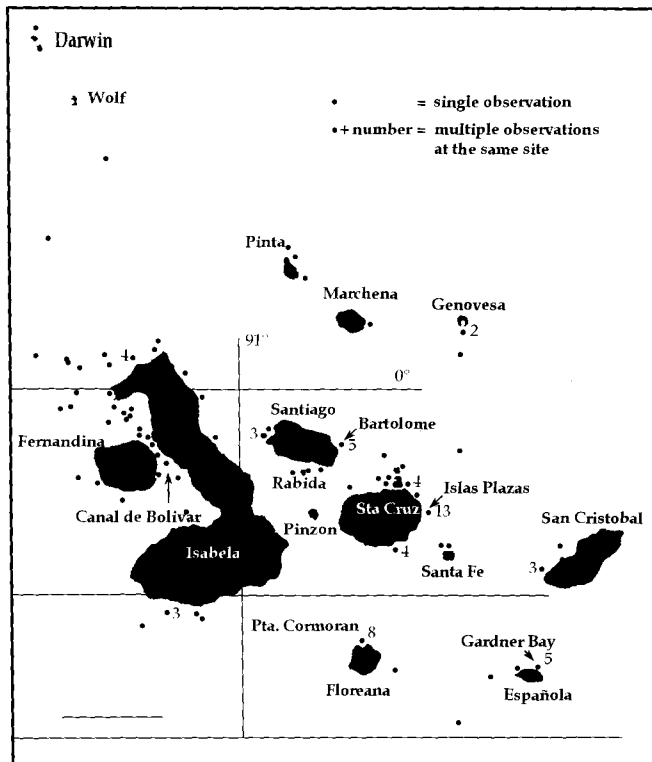


Figure 2. Map of the Galápagos Archipelago, indicating distribution of orca sightings. Sightings 29, 38, 41, and 53 are not included as being outside the scope of the map.

## CONCLUSION

The orca in Galápagos remains, to a large extent, an enigmatic animal. Nevertheless, a long-term monitoring program will provide information that allows a small window to be opened into the lives of these powerful predators. Their importance in the general ecosystem remains unclear. The fact that large numbers of resident pinnipeds and small dolphins are found in and near the Archipelago, both of which fall prey to orcas, leads to the unanswered question: what are the controlling factors for the orca population in Galápagos? Does a resident population exist? There is also the unanswered question of whether orcas feed at night, for at that time many species of dolphins and the Galápagos fur seals are highly vocal, suggesting an easy target for sonar-equipped orcas.

Providing the population sizes of their prey species are maintained, it seems that orcas will continue to grace the waters of Galápagos. However, should certain fishing techniques, such as net-fishing for sharks, become common in bays where orcas are known to fish, entanglements may start to occur. Should the orcas be transients, then there is the hope that they will not learn to remove fish from hooks from an increasing longline fleet and become the subject of the fisherman's ire and revenge.

## ACKNOWLEDGMENTS

I would like to express my appreciation to all the National Park Guides who have dedicated their time to filling out the sighting forms. Without their help, information on orcas would be little more than hearsay. At the same time, I would like to thank all those who have helped with information on orcas. Mention must be made of Dr. Hal Whitehead for his unwavering help, and I would like to thank Daniel Palacios for sharing his unpublished orca database, which contained information difficult of access. I would also like to express my thanks to Eduardo Diez (Quasar Nautica) for his continuing support of my projects. I thank Dr. Rodrigo Bustamante for his helpful review of an earlier version of this manuscript. The Galápagos National Park Service, under the direction of Biol. Eliecer Cruz, and the Instituto Nacional de Pesca (INP) have maintained their support for ongoing research into marine mammals in Galápagos.

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## APPENDIX

The 135 sightings are listed in chronological order, with information on date, location, and pod composition.

The **date** is given as precisely as was known. The **location** is generally given as the location where the orcas were first seen. Sometimes orcas were followed for some time and thus changed their position. For the purpose of this report, it was felt generally preferable to name locations rather than degree and minute positions, as the animals are often very close to shore and



difficult to pinpoint by the latter method.

In the column entitled **Composition**, the first figure is the total number of animals observed. Thereafter follows the sex and age composition, if known. *Mature males*, for example, are shown thus: 2m. (= two mature males). Because it is generally impossible to differentiate between females and young males, *all smaller animals*, except obvious calves, are marked thus: 3f. (= three females or young males). *Calves*, much smaller animals and often swimming close to an adult, suspected to be its mother, are marked thus: 1c. (= one calf).

Under the composition title, attacks, or potential

attacks, if they occurred, are marked with an *asterisk* (\*).

A species name following the orca pod composition indicates the animal being harassed (that is, not seen to be touched), bitten, or eaten. A *single asterisk* \* indicates an harassment. *Double asterisks* \*\* indicate observed bites, blood, or prey being eaten.

Attempts have been made to improve sighting accuracy by a publication (Merlen 1995), through the greater availability of guide books in general, and through the National Park's guide training courses. However, occasional misidentifications cannot be ruled out and some compositions may be imprecise. Nevertheless, the accuracy is considered to be high.

### APPENDIX 1. CHRONOLOGICAL LIST OF ORCA SIGHTINGS.

	Date	Location	Composition
1.	1948 +	Near Santa Fe	3.
2.	1950 +	Puerto Ayora, Santa Cruz	1
3.	1950s	Gardner Bay, Española	1.
4.	1959	Wreck Bay, San Cristóbal	2.
5.	1959	Canal de Bolívar, Isabela	2.
6.	1960 September	Punta Espinosa, Fernandina	1.
7.	1961 February	Post Office Bay, Floreana	1.
8.	1961 November	Wreck Bay, San Cristóbal	1.
9.	1961 December	Pta. Albermarle, Isabela	3.
10.	1961 December	Darwin Bay, Genovesa	5.
11.	1976 January 29	00°11.3'N 91°48.5'W	4.
12.	1976 December 1	Bartolomé, Santiago	1. 1m.
13.	1978. April 3	Punta Cormorán, Floreana	3. 1m. 1f. 1c.
14.	1978 June 12	Canal de Itabaca	2. 1m. 1f.
15.	1978 August 13	00°33.6'S 90°06.5'W	4.
16.	1978 August 13	00°44.9'S 90°09.6'W	1.
17.	1979 June 10	Gardner Bay, Española	1. 1m. Sealion **
18.	1979	Darwin Bay, Genovesa	2. Hammerhead shark **
19.	1980 January 28	00°25'S 90°20'W	1.
20.	1980 April 16	Punta Cormorán, Floreana	3. 1m. Manta ray **
21.	1980 April 23	Bartolomé, Santiago	1.
22.	1980 April 24	Espumilla Beach, Santiago	1.
23.	1980 May 1	Plaza Islands	1.
24.	1980 May 5	Caleta Tortuga, Santa Cruz	1.
25.	1980 July 7	00°17'N 89°57'W	3. 1m. 1f. 1c
26.	1981 February 4	00°37'S 90°10'W. (Plaza Islands)	2. 2.m.
27.	1981 June 12	00°19.4'S 90°20.8'W	2.
28.	1981 June 15	02°13.3'S 92°29.9'W	48.
29.	1981 June 15	02°18.1'S 92°03.2'W	2.
30.	1981 August 7	Canal de Itabaca	1+.
31.	1981 August 13	00°17'S 90°34'W, Bartolomé	3.
32.	1981 September	00°17'S 91°21'W, C. de Bolívar	2.
33.	1981 October	00°28'S 90°28'W	1.
34.	1981 November 15	00°34'S 90°10'W, Plaza Islands	1.
35.	1982 January 8	02°05'S 84°34'W	3-4. 8 sperm.
36.	1982 January 12	00°25'S 91°23'W, C. de Bolívar	1. 1m
37.	1982 January 21	Santiago, Espumilla Beach?	1.
38.	1982 January 22	01°05'S 91°12'W	1.
39.	1982 January 24	Santiago, Puerto Egas?	2.
40.	1982 January 26	00°29'S 90°16'W, C. de Itabaca	1.



41.	1983 January 22	Plaza Islands, Santa Cruz	1.
42.	1983 April 16	Canal de Bolívar	1.
43.	1983 October 10	South Plaza Island, Santa Cruz	1. Manta **
44.	1983 November 17	01°43'S 83°56'W	2.
45.	1985 January 17	Punta Cormorán, Floreana	1.
46.	1985 April 10	Bartolomé, Santiago	1.
47.	1985 April 18	00°57'S 93°07'W	20+. 3m. Sperm ** 15-20f. 2c.
48.	1985	South Plaza Island, north shore	1. 1m. sealion **
49.	1986 January 28	Inside Tagus Cove, Isabela	2. 1m. 1f.
50.	1986 February 4	Pta. García, Isabela, 1 n.m. to S.	1.
51.	1986 May 15	Baltra Harbor, Baltra	1. 1m
52.	1986 November 16	00°29.1'N 92°11.0'W	1.
53.	1987 May 29	00°10'N 91°48'W	5. 2m. 3f.
54.	1987 June 2	00°49'N 91°52'W	4.
55.	1988 October 11	00°10.0'N 91°28.0'W	1.
56.	1988 December 21	00°09.0'S 91°37.0'W	1.
57.	1988 December 21	00°05.0'S 91°48.0'W	2.
58.	1989 January 3	Puerto Ayora, Santa Cruz	2.
59.	1989 January 17	00°11.0'S 92°34.0'W	10.
60.	1989 January 21	00°06.0'S 91°52.0'W	6.
61.	1989 January 27	01°22'S 89°54'W	1.
62.	1989 March 1	00°45.0'N 90°46.0'W	8.
63.	1989 March 22	Banks Bay, Isabela	8. 1m. Common dolphins *
64.	1991 December 12	Punta Espejo, Marchena	6. 1m. 3f. 2c. Snappers *
65.	1991	Puerto Ayora, Santa Cruz	2. Sting ray **
66.	1991 January 17	Sombrero Chino, Santiago	2. 2f. Manta **
67.	1991 March 7	02°44'S 81°56'W	3. 1m. 2f. 12 sperm
68.	1991 March 23	00°13'N 91°36'W	3. 1m. 2f.
69.	1991 April 5	00°07'S 90°37'W	8. 1m. 5f. 2c. 20+ sperm
70.	1991 April 14	00°20'S 89°58'W	6. 2m 2-3f. 1c.
71.	1992	Punta Espinosa, Fernandina	6.
72.	1992. May	Pta. Vicente Roca, 2 n.m. to S.	4. Cuvier's beaked whale **
73.	1992 August (late)	South Plaza Island, east point	2.
74.	1992 September 25	Santa Fe, NW point	1. 1m.
75.	1992 September 30	Santa Cruz, NE coast	3. 1c.
76.	1992 November 5	Gardner Bay, Española	1. 1m.
77.	1993 February 4	Gardner Island, Floreana	1. 1m.
78.	1993 July 19	Gordon Rocks, Santa Cruz	1. 1m.
79.	1993 July 25	Gordon Rocks, Santa Cruz	2.
80.	1993 August 3	Puerto Egas, Santiago	4.
81.	1993 August 3	00°09.0'S 92°29.8'W	5.
82.	1993 August 5	NE Baltra, Santa Cruz	3. 1m.
83.	1993 August 6	Buccaneer Bay, Santiago	1. 1m.
84.	1993 August 15	00°00.9'S 91°44.8'W	4.
85.	1993 August 19	Punta Cormorán, Floreana	1.
86.	1993 August 19	Punta Cormorán, Floreana	1.
87.	1993 October 25	00°09'S 91°33'W, Banks Bay	10. 2m. 5 Rorqual. <i>B. edeni</i> **
88.	1993 October 26	00°29'S 91°45.5'W	8. 1m. 3f. 1c. 12 sperm **
89.	1993 November 13	00°35.8'S 91°34.0'W	2.
90.	1993 December 11	Rábida, west side	2. 1f. 1c.
91.	1994 February 4	Cape Marshall, Isabela	1.
92.	1994 February 23	Plaza Islands, Santa Cruz	2.
93.	1994 February 26	Canal de Itabaca, E entrance	2. 1m. 1f.
94.	1994 March 4	00°11'N 92°02'W	10-15. Cuvier's beaked whale**
95.	1994 April 4	Post Office Bay, Floreana	3. 1m. 1f. 1c.
96.	1994 April 10	North Plaza Island, north coast	3.
97.	1994 June 17	Fernandina, south coast	5. 1m. 2f. 2c. Turtle **



98.	1994 July	Darwin Island, 1 n.m. to north	5+. 1m. shark **
99.	1994 November 3	Gardner Bay, Española	6. 1m. 1f. 3c.
100.	1994 November 24	Gardner Bay, Española	1. 1m.
101.	1994 December 15	Plaza Islands, Santa Cruz	2.
102.	1995 February 17	Wolf Volcano, Isabela, east coast	8. Manta ray **
103.	1995 March 20	North Plaza Island, north coast	6. 1+m.
104.	1995 April 4	Punta Cormorán, Floreana	3.
105.	1995 April 9	01°50'S 90°02'W	5. 3m. 1f. 1c.
106.	1995 April 20	01°08'N 91°44'W	5. 5f. 2c.
107.	1995 June 13	00°11'S 91°30'W, Banks Bay	2-4.
108.	1995 July 15	Kicker Rock, San Cristóbal	1. 2 Rorquals *
109.	1995 July 19	Banks Bay, Isabela	2-4. Manta ray. **
110.	1995 August 11	Puerto Egas, Santiago	4. 1m. 3f. Sealions *
111.	1995 August 28	Wreck Bay, San Cristóbal	3. 1m. 1f. 1c.
112.	1995 September 7	00°09'N 91°44'W	6. 6f. Common dolphins **
113.	1995 September 10	Rábida, red beach	3. 1m. 2f.
114.	1996 January 13	Puerto Egas, Santiago	1. 1m.
115.	1996 January 14	Punta Flores, Isabela	3. Sunfish *
116.	1996 January 17	00°10'N 91°37'W	2. 2f. Bottle nosed dolphin **
117.	1996 January 19	Punta Flores, Isabela	6-7. 2m.
118.	1996 January 26	Caleta Derek /Fragata, Isabela	2. 2f.
119.	1996 January 26	Urvina Bay, Isabela	3. 3f.
120.	1996 January 27	South of Cerro Azul, Isabela	2-3. 1m.
121.	1996 February 24	01°12'S 91°30'W	6. 1m. 3f. 2c. 50 + Pilot whales *
122.	1996 March 27	South of Cerro Azul, Isabela	4. 2m. 2f. 1c.
123.	1996 April 17	South of Cerro Azul, Isabela	5. 1m.
124.	1996 April 21	00°15'N 91°24'W	4. Common dolphins *
125.	1996 April 28	Cape Rose, Isabela	3-4. 12 Sperm *
126.	1996 August 18	00°02'S 91°36'W	1. 1m.
127.	1996 August 21	Puerto Ayora, Santa Cruz	2. 1m. 1f.
128.	1996 September 21	Punta Flores, Isabela	9.
129.	1996 November 22	Daphne Islands	3.
130.	1996 December 3	Darwin Island	3.
131.	1996 December 31	Bartolomé, 2 nm to East	6. 2m. 2f. 2c.
132.	1997 January 2	Punta Albemarle	3. 1m. 2f.
133.	1997 January 29	00°41.5'N 90°44.0'W	8. 1m. 6f. 1c.
134.	1997 January 29	00°31.9'N 90°41.2'W. Pinta	4. 1m. 3f. Feeding. Prey?
135.	1976-1983	Cape Hammond, Fernandina	3-5. Fur seal **

TOTAL=135 sightings



## REEF FISH BEHAVIOR DURING A TOTAL SOLAR ECLIPSE AT PINTA ISLAND

Simon Jennings, Rodrigo H. Bustamante, Ken Collins, and Jenny Mallinson

At 10.59 hours (Ecuadorian Time) on 26 February 1998 there was a solar eclipse at Pinta Island, Galápagos (Espenak and Anderson 1997; Figure 1). The eclipse began when the sun was at an altitude of  $68^\circ$  and the period of totality (sun completely obscured by the moon) lasted 3.5 min. Light levels during totality were equivalent to those at night, and planets and stars were visible to the human eye. The eclipse provided an opportunity to observe the effects of changes in light intensity on the behavior of reef fishes.

Reef fishes can be categorised as diurnal, nocturnal, or crepuscular (Hobson 1965, 1972, McFarland 1991). In late morning, on reefs close to the equator, only diurnal fishes are active and nocturnal or crepuscular fishes are sheltering within crevices or caves. The behavior and abundance of reef fishes was recorded before, during, and after the eclipse in an area of 10 m by 2 m at a depth of 7-10 m on the reef slope north of Pinta Island (Figure 1,  $00^\circ 37.77' N$ ,  $90^\circ 45.32' W$ ). The study area consisted of a volcanic boulder slope with c. 15% massive coral and 2% branching coral cover. All fishes >5 cm LT swimming in open water above the reef were

counted at 5 min intervals from 10.20 until 10.45 hours and then counted before, during, and after totality. Each census took 2-3 min. Divers also made behavioral observations at depths of 2-15 m on the same reef.

Eight diurnal species: the anthias (Serranidae) *Paranthias colonus* (Valenciennes), the wrasse (Labridae) *Bodianus diplotaenia* (Gill), the damselfish (Pomacentridae) *Stegastes beebei* (Nichols), the hawkfish (Cirrihitidae) *Cirrhilichthys oxycephalus* (Bleeker), the angelfish (Pomacanthidae) *Holocanthus passer* Valenciennes, the butterflyfish (Chaetodontidae) *Johnrandallia nigrirostris* Gill and the grunt (Haemulidae) *Anisotremus interruptus* (Gill) were observed in the 20 m<sup>2</sup> study area. The nocturnal squirrelfishes (Holocentridae) *Myripristis leiognathos* Valenciennes and *Adioryx suborbitalis* (Gill) were sheltering in crevices.

Clear changes in the behavior of diurnal fishes were observed at 10.55 hours, 4 min before totality. At this time light levels had fallen to < 1 % of those in unobstructed sunlight at the same time of day. Plankton-feeding *P. colonus* started to descend from the shallow study area towards the reef edge and other species stopped feeding and retreated to crevices between the boulders and corals. Hawkfishes sheltered within branching corals. When the area was censused during totality (Figure 2), no diurnal fishes were swimming above the reef.

All species within the study area remained in shelter during totality, with the exception of some *P. colonus* which formed tight schools on the reef edge. There was no sign of nocturnal squirrelfishes emerging from the reef and they shared crevices and caves with diurnal species. Totality ended shortly after 11.02 hours and diurnal fishes returned to areas above the reef within 3 min. At this time fishes were as abundant above the reef as they had been 14-39 min prior to the eclipse (Figure 2). Seven minutes after totality, all species in the study area had been observed feeding.

The behavior of other species was observed outside the 20 m<sup>2</sup> study area. In deeper water (12-15 m), some nocturnal species such as the glasseye *Heteropriacanthus cruentatus* (Lacepède) and *Myripristis* spp. started to leave the shelter of caves and crevices. The diurnal parrotfishes (Scaridae) *Scarus ghobban* Forsskål and *Scarus rubroviolaceus* Bleeker stopped feeding 3 min before totality and resumed feeding 4 min after totality. During totality the parrotfishes sheltered in the reef as at night. The only diurnal species which did not exhibit typical night-time behavior during the eclipse was the surgeonfish (Acanthuridae) *Prionurus laticlavus*

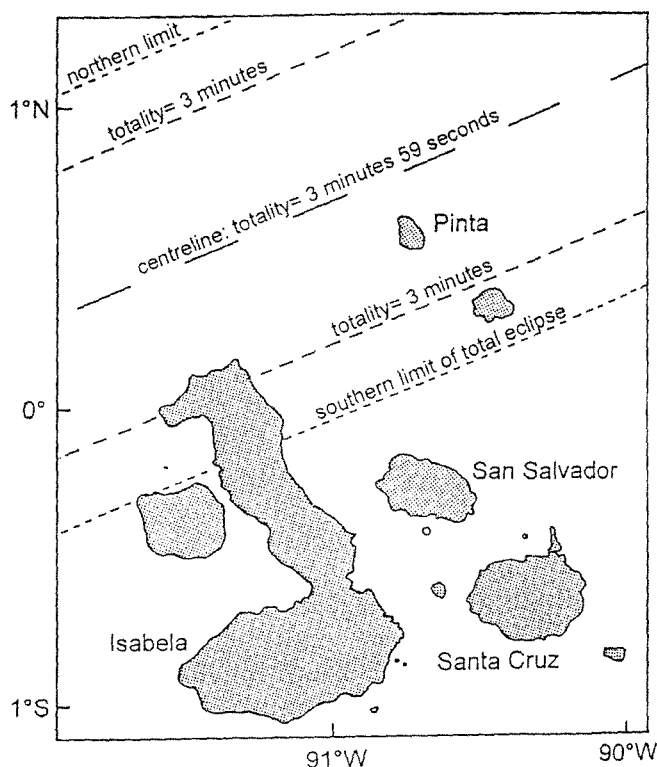


Figure 1. Map of Galápagos showing limits of total eclipse.

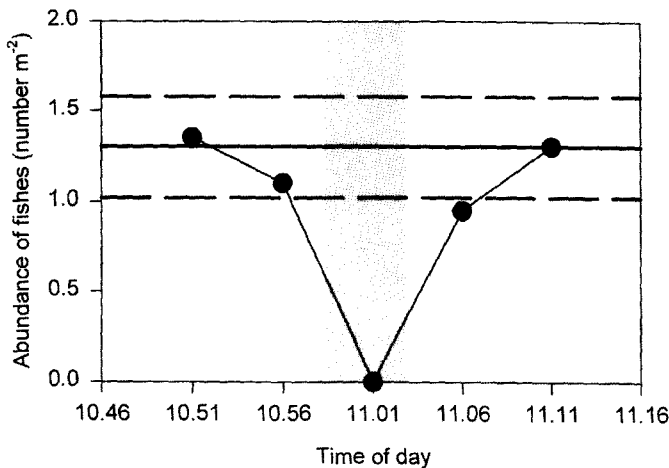


Figure 2. Abundance of fishes prior, during, and after the eclipse.

Valenciennes, which stopped grazing on algae in the surge zone approximately 4 min before totality and formed large tight schools, which swam with alarm and rapid changes in direction throughout the eclipse period. *Prionurus* continued this disturbed shoaling behaviour for 2 min after totality and did not resume grazing for another 5 min. All other species of planktivorous, herbivorous, and invertebrate-feeding fishes appeared to have adopted normal day-time behavior before this time.

The relatively slow rate of descent of fishes towards the reef at dusk is considered to be a function of the relatively slow decrease in light level (Hobson 1991, McFarland 1991). The rate of descent is governed by the trade-off between maximizing feeding rate and minimizing the risk of being attacked by predators (Hobson 1991). Our observations support the hypothesis that the behavior of diurnal reef fishes at dawn and dusk is a direct response to light level. The rapid decrease in light level during the brightest period of the day did not elicit a response noticeably different from that usually observed at dusk, but movement towards shelter provided by the reef was simply accelerated. The only species which did not respond as if subjected to a normal day-night cycle was the grazing surgeonfish *Prionurus*. Their alarmed shoaling response may have resulted from the presence of sea lions in the surge zone. The sea lions swam actively in this area throughout the eclipse, whereas they would do so rarely at night.

Studies of other animals during eclipses also demonstrate a direct response to decreased light intensity and the rapid adoption of night-time behavior. Ransome (1927) reported that brown trout *Salmo trutta* L. stopped feeding for approximately 20 min after an eclipse in the United Kingdom and Uetz *et al.* (1994) demonstrated that colonial orb-weaving spiders began to take down their webs (as they do at night) during the Mexican eclipse in 1991. Similarly, lizards reverted to

typical night time behavior during this eclipse (Ortegarubio *et al.* 1994). The next total solar eclipse will occur on 11 August 1999. The path of the moon's umbral shadow will cross marine and freshwater sites from south-west England to the Bay of Bengal.

## ACKNOWLEDGEMENTS

We thank David Day and Heidi Snell for information on the solar eclipse, the captain and crew of the RV *Beagle* for logistic support, the Galápagos National Park Service for research permits, and the Department of Environment, Transport and Regions (DETR) Darwin Initiative for funding.

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# THE 1997-98 EL NIÑO IN GALÁPAGOS: CAN 34 YEARS OF DATA ESTIMATE 120 YEARS OF PATTERN?

Howard Snell and Solanda Rea

## INTRODUCTION

The 1997-98 El Niño event missed being the wettest two-year period in the Galápagos Archipelago by less than one millimeter. Between 1 January 1997 and 31 December 1998, 3407.6 mm of rainfall was recorded at the Charles Darwin Research Station on Santa Cruz Island. That is 19% of all the rainfall since 1965, a total surpassed only by the El Niño event of 1982-83, when 3408.2 mm of rain fell (also 19%, Table A.1). Across most of the eastern Tropical Pacific Basin, the 1997-98 El Niño appears to have been the strongest in recorded history (Kerr 1999, McPhaden 1999). While the difference in total rainfall on Santa Cruz between the two El Niños is less than two-thousandths of one percent, most residents and visitors of the Galápagos who experienced both events recall that of 1982-83 as being much more severe. Does memory fail us or are patterns within the Galápagos distinct?

On the large scale, El Niño events are associated with abnormally high and consistent sea-surface temperatures across the tropical Pacific. The lack of the normal west-to-east thermal gradient across the surface of the Pacific is coupled with the weakening and occasional reversal of the easterly tradewinds. A combination including high sea-surface temperatures and weak winds promotes tremendous evaporation of water into the atmosphere, leading to abnormally strong convective storms and great rainfall (McPhaden *et al.* 1998). Generally El Niño events last between 12 and 18 months (McPhaden *et al.* 1998). For the last 5000 years these conditions have occurred approximately every 2 to 8.5 years, roughly double the rate during the 10,000 prior years (Robell 1999). The intensity of the rainfall and the thermal anomalies occurring during El Niño events appear to be increasing within the last twenty years (Wolter and Timlin 1998). While global warming may influence that increase, it appears that several recent El Niños, including those of 1982-83 and 1997-98, coincided with other cyclical climatic events of greater temporal amplitude that may have magnified their intensities (Kerr 1999). El Niño events are apparently part of a cycle that often includes a subsequent dry period that can develop into severe droughts. Recently these dry periods have been called La Niña events (McPhaden *et al.* 1998).

These climatic fluctuations are powerful factors in the ecological interactions of many species within the Galápagos and elsewhere (Robinson and del Pino 1985, Grant 1985, other articles in this volume). The general

impression is that terrestrial organisms flourish during the wet Niño conditions and suffer the droughts of La Niñas, while marine species suffer during the Niño periods of high sea-surface temperatures and decreased upwelling of deep, nutrient-rich ocean currents and prosper during "normal" and La Niña conditions. However, several species of terrestrial organisms appeared to suffer higher than usual mortality and low reproductive success during the 1997-98 El Niño event. Additionally, several alien aggressive terrestrial species increased their ranges during the same time. It is possible that the combinations of reduced reproductive success, increased mortality, and spread of alien species could make modern El Niño events damaging for terrestrial organisms. Within this paper we examine patterns of climatic variability within the Galápagos and compare them with patterns of the eastern tropical Pacific and continental Ecuador as a framework for evaluating potential biological consequences.

## METHODS

Data for this study came from direct measurements, the published literature, and the Internet. Basic meteorological variables have been measured by the Charles Darwin Research Station (CDRS) since 1964. We use mid-day air ( $T_a$ ) and sea ( $T_s$ ) temperatures and total daily rainfall (1800-1800, all times are UTC - 6 hr) from 1 January 1965 through 31 December 1998. Air temperature is recorded in shade 2m above the surface,  $T_s$  is recorded at the coast in a bucket of water pulled from the sea, and total daily-rainfall is the sum of measurements taken at 0600, 1200, and 1800 from a rain gauge 1.5 m above the surface. The coastal station is on the grounds of the CDRS at 0° 44' 20" S latitude, 90° 18' 25" W longitude. Since 1987, measurements have been recorded from a station in the upper Transition Zone (Bellavista, 194 m altitude) at 0° 42' S latitude, 90° 22' W longitude. We produced monthly averages or totals of these data with pivot tables in Microsoft Excel 97. Accumulated rainfall is the inclusive sum from January to the month represented. Because El Niño events often span two calendar years, we needed an additional set of two-year periods for comparisons. We produced a set of 33 periods using all pairs of successive years. This requires that each year be represented twice, once as the first year of a period and once as the last year of a different period. That set includes all potential El Niño and La Niña events.

Some published data for the tropical eastern Pacific were extracted from figures downloaded from the Internet (McPhaden 1999, Wolter and Timlin 1998, Robell *et al.* 1999). The figures were imported into ArcView 3.1 (Anonymous 1996), referenced to a coordinate system based on their axis, and the data exported to an Excel 97 spreadsheet. Additional data were downloaded directly from web sites of the National Oceanic and Atmospheric Administration's (NOAA) web pages and the Comprehensive Ocean-Atmosphere Data Set (COADS, ) within the Internet Data Library of the International Research Institute for Climatic Prediction (IRI, [www.iri.ideol.columbia.edu](http://www.iri.ideol.columbia.edu)).

## RESULTS AND DISCUSSION

### *Climatic patterns*

Annual rainfall is extremely variable in the arid coastal zone of Galápagos (Figure 1). The coefficient of variation among years is 107.6, and the distribution is

highly skewed towards a few years with extremely great rainfall ( $g = 2.412$ , Table A1). The wettest year recorded since 1964 is 1983 and the driest 1985 (2769 and 64 mm, respectively, Table A1). Although we have not encountered data demonstrating years with greater rainfall, drier periods have been recorded on San Cristóbal and Daphne (Grant 1985, rainfall measured January through May). However, apparent differences in values from data sets covering the same site and years have led us to revise previously distributed data from the CDRS, and it is possible that there were similar problems in previous data from San Cristóbal. Regardless, a range of total rainfall among years of 2705 mm is great. Unfortunately, rainfall was not recorded at Bellavista during 1983, so we do not know how much rain fell there. Generally, Bellavista receives approximately 500 mm more rain than the CDRS, and that difference is relatively independent of the total amount of rain (Figure 2). Thus, the coastal region does not receive a constant percentage of the rainfall in the upper transition zone, rather it gets, on average, about

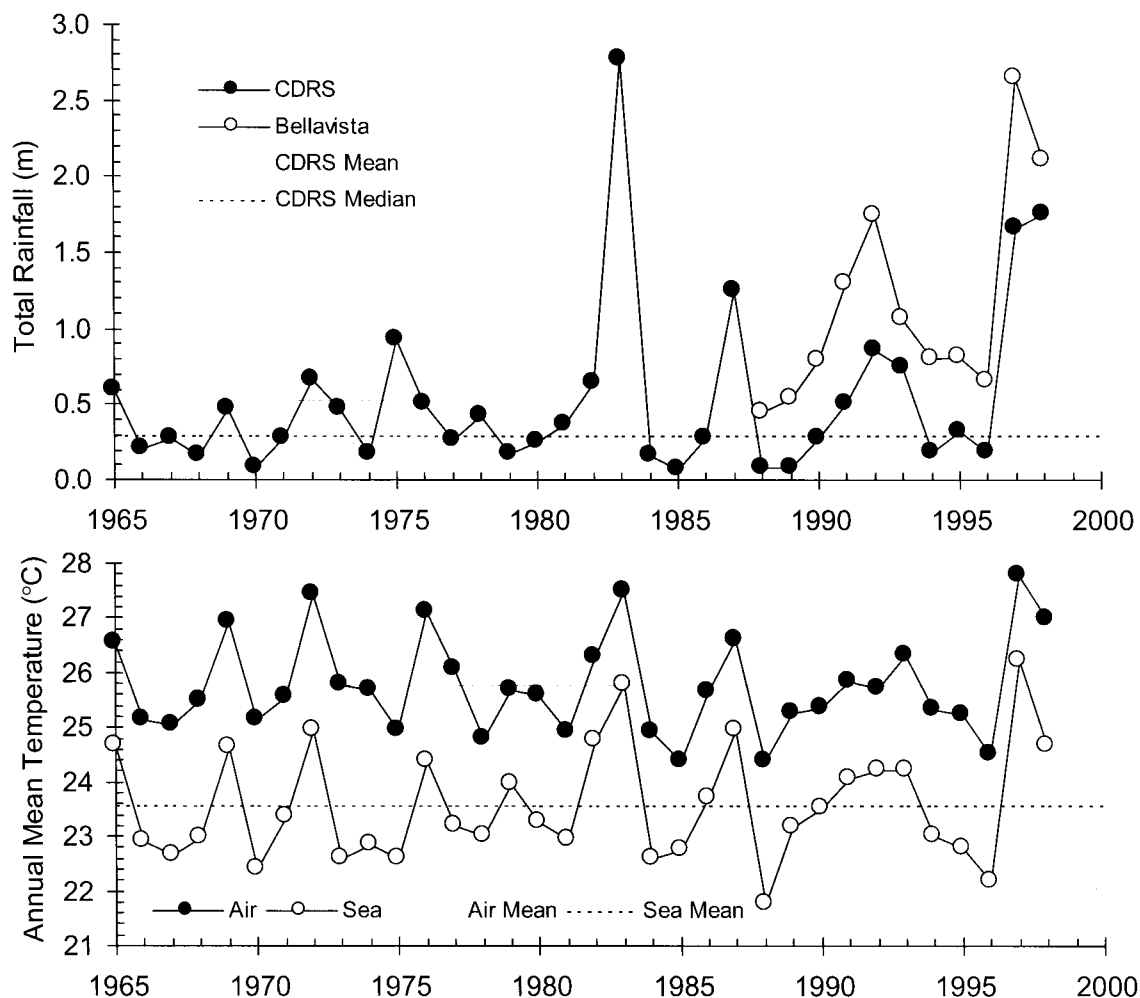


Figure 1. Rainfall and temperature patterns on Santa Cruz Island.



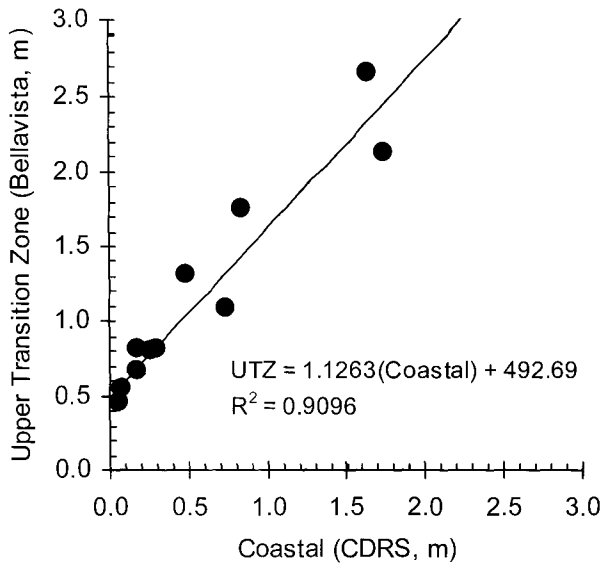


Figure 2. Relationship of coastal and upper transition zone rainfall on Santa Cruz Island.

13.5% in dry years and 71% in the wettest years. Not only is rainfall greater in the upper transition zone, it is less variable (coefficient of variation = 64.03) and less skewed towards years with great rainfall ( $g = 1.128$ , Table A2).

Since 1965, there have been five strong El Niño events in Galápagos: 1975-76, 1982-83, 1986-87, 1993-94, and 1997-98 (Figure 1). Although recorded as a strong El Niño event elsewhere, 1972 and 1973 showed barely abnormal rainfall in Galápagos (Figure 4). The year 1965 was also recognized as an El Niño event (Grant 1985), although, in view of the amounts of rainfall recorded in El Niño events since 1975, the 600 mm recorded then seems slight. The only El Niño recorded in Galápagos that did not result in two years of above-median rainfall was that of 1986-87 (Figure 1). Within Galápagos, it could be appropriate to view that as an event of a single year (1987), but its signal in other parts of the Pacific was that of a typical El Niño event extending into two calendar years (McPhaden 1999). The recorded El Niños of Galápagos are always followed by droughts. If we define a drought as the span of contiguous years with rainfall below the median, the average duration of post-Niño droughts is 2.3 years and the mode is 3 years. The 1980s were a decade of extremes for the islands. The two most severe droughts and the first- and third-ranked El Niños occurred then.

While the total amounts of rainfall in the 1982-83 and 1997-98 El Niños are effectively identical (Table A1), they differed greatly in medium-term intensity. Although the rainiest day ever recorded at the CDRS was 3 June 1997 (194.6 mm), the monthly totals in 1983

are incredible. During the three months of April, May, and June 1730 mm of rain fell, surpassing the totals of all years except 1998 (Table A1). Apparently a "typical" El Niño does not exist for the Galápagos. Even though strong El Niños in the Galápagos basically accumulate either 3.4 or approximately 1.5 m of rain, the patterns of rainfall-accumulation and the sea-surface temperature anomalies producing them are variable. Some events accumulate rain during the typical rainy seasons, January through April (Table A1) of two years. That pattern was shown in 1975-76 and 1992-93. Other events accumulate rain during the normal rainy season and receive extraordinary rainfall in typically drier months (1982-83, 1986-87, and 1997-98). In general, El Niño events with great rainfall have larger  $T_s$  anomalies for longer periods than those with less rainfall (Figure 3). It is difficult to establish the "normal" pattern for climatic variability in the Galápagos Islands when nearly one-third of the years with recorded data are involved in El Niño events and another third are La Niña droughts (Figure 1). Nine months of the year have coefficients of variation for rainfall that exceed 100% (November through July), leaving three months that are predictably dry, at least in the coastal regions (August, September and October, Table A1). The "normal" pattern may simply be that rainfall can occur from January through April in "non-Niño" years and that the misty precipitation of the garúa season will provide little moisture in July through October. The months of November, December, and May to July usually experi-

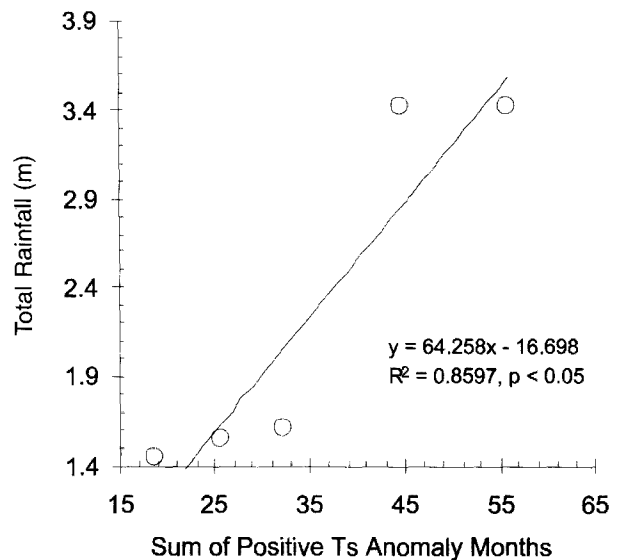


Figure 3.  $T_s$  anomaly and accumulated rainfall during El Niño events in Galápagos.

ence little rainfall or garúa except in El Niño years, when they can have from 150 to 660 mm of rain (Table A1).

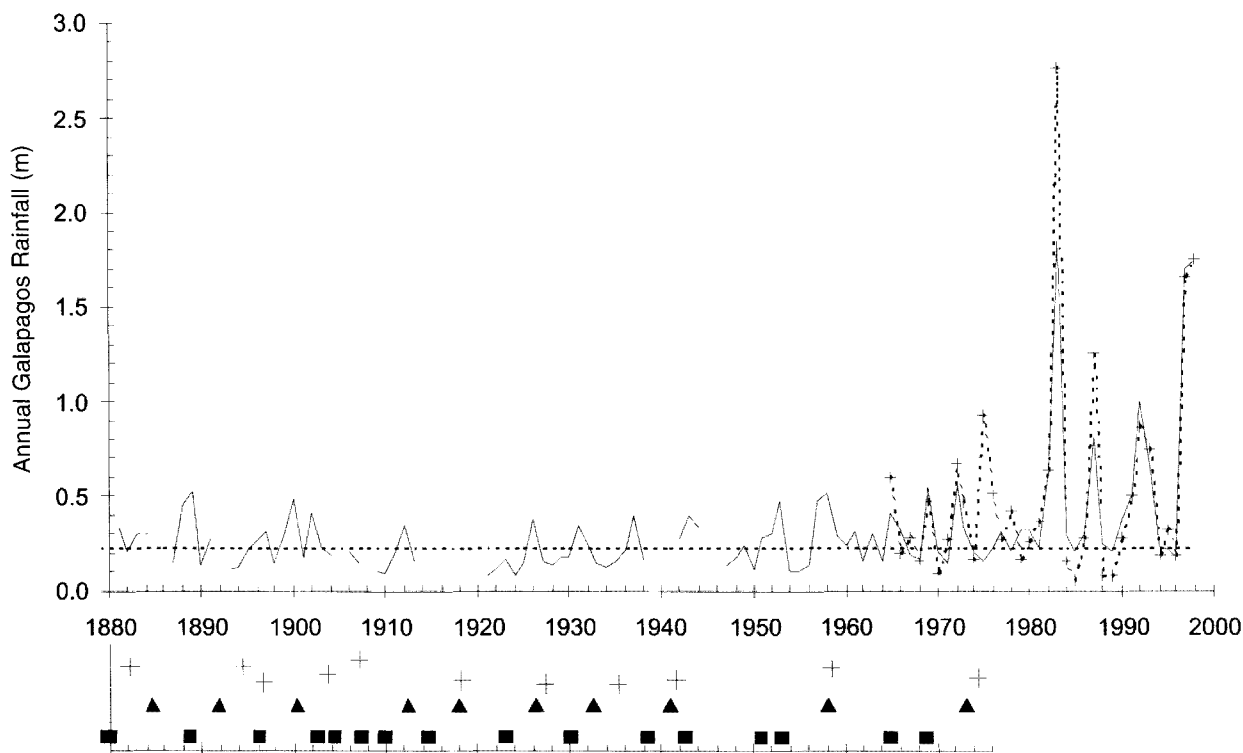
The frequency of strong oscillations between wet and dry periods (El Niño – La Niña cycles) during the last 34 years is roughly once in seven years. Including weaker oscillations (1965, 1972-73) drops the frequency to once every five years. The periodicity of oscillations appears relatively similar through the 34 years, but the tendency for the oscillations to be extreme is increasing significantly. The annual totals of rainfall in the second half of the period are significantly more variable than those of the first half (1982-98 standard deviation = 757.1, 1965-1981 standard deviation = 219.0,  $p = 0.02$ , Levene's Test). This follows a pattern of increasingly strong El Niño events observed across the tropical Pacific region since 1975 (Wolter & Timlin 1998).

Is this increase in Galápagos part of a long-term trend? As of 1972, the conditions in Galápagos were apparently as wet as any period in the preceding 50,000 years and were relatively consistent for the last 3,000 years (Colinvaux 1972, reported in Grant 1985). To examine trends over a shorter period in more detail, we have constructed an estimated history of oscillations in the Galápagos over the last 118 years (Figure 4). This estimated history is based on a record of sea-surface temperatures for the tropical Pacific (Slutz *et al.* 1985)

and compared to a record established from sediments deposited in a montane lake of southern Ecuador (Robell *et al.* 1999). We estimated the monthly rainfall of Galápagos from a polynomial regression ( $r = .69$ ,  $p < 0.001$ ) and summed the monthly values into an annual total. The estimated total annual rainfall agrees well with the observed values over the last 34 years (Figure 5).

The frequency of oscillations is relatively constant during the last 118 years and appears similar to the current frequency (12 oscillations in 67 years with sufficient data yields an oscillation every 5.6 years). If we divide the history into three periods of past (1880-1964), recent (1965-1981), and current (1982-1998), we can examine the possible trend. The current total annual rainfall is greater than the recent and past amounts, and the recent and past do not differ significantly (Tukey's HSD: current  $p < 0.0001$ , recent and past  $p = 0.325$ ). Variability increases significantly from the past through the recent to the present periods (past standard deviation = 129.2, recent and current values presented above; Levene's Test,  $p < 0.02$ ). Thus, for the last 118 years, it appears that the amounts of rainfall and the strength of El Niño events remained relatively constant until the current period, when the amounts of rain during El Niño events increased. If these estimated patterns reflect the real trends, the Galápagos Archipelago could be entering one of the wettest periods in its history.

Figure 4. Estimated pattern of Galápagos rainfall between 1880 and 1998. Squares and triangles indicate, respectively, moderate and severe El Niño events, as determined from historical records. Plus signs indicate El Niño events as determined by a study of organic deposits in an Andean lake.





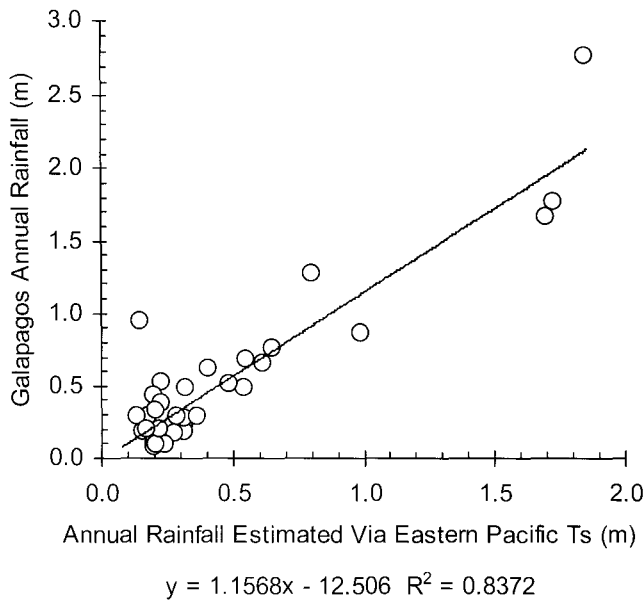


Figure 5. Predictability of annual Galápagos rainfall.

### Biological consequences

Many species associated with the marine ecosystem of Galápagos greatly declined in numbers during the 1997-98 El Niño (details of many of the following examples are reported in other papers of this volume). Dead sea lions and marine iguanas became common sights throughout the islands and their numbers may have dropped to less than half of the totals present prior to 1997. Galápagos penguins declined to levels similar to those seen after the 1982-83 El Niño and standardized counts made during 1998 recorded the fewest penguins ever seen. Many other species of seabirds failed to reproduce and may have experienced increased mortality of adults.

Some terrestrial organisms may have responded differently than their marine counterparts, although others appeared to suffer. The population of dark-billed cuckoos on Santa Cruz apparently exploded and may have peaked in July and August of 1998. The population crashed immediately after, and reports of dead cuckoos in the highlands were frequently received at the offices of the CDRS and the Galápagos National Park Service. Several populations of Galápagos tortoises failed to reproduce under natural conditions. In some cases, it appears that increased vegetation and wet soils dropped the nest temperatures to values lower than the embryos could survive (Steve Earsom, pers. comm.). In other cases, increases in populations of introduced fire ants (*Solenopsis*) attacked and killed hatchling tortoises within their nests. Mortality of adult tortoises increased several fold on Alcedo

Volcano, Isabela Island, where more than thirty individuals were killed in floods or by falling down the freshly cut banks of steep ravines (Cruz Márquez, pers. comm.).

### Introduced species

The unique biological diversity of the Galápagos Islands is an evolutionary product of the Archipelago's isolation. Prior to the beginning of human activity within the islands in 1535, the barriers that maintained that isolation were the difficulty that most species faced in crossing at least 1000 km of ocean and the problems associated with colonizing an arid set of sparsely vegetated islands. For the last several hundred years the difficulties of dispersal have been removed by the numerous arrivals of boats and airplanes into the archipelago. Thus some 400 to 500 species of plants, some 25 vertebrates, and unknown hundreds of invertebrates have been introduced to compete with and prey upon the natural flora and fauna of the islands. However, many more species have failed to establish themselves once they reached the islands because of the dry conditions usually found in the Archipelago. During the 1997-98 El Niño, it became obvious that the situation is changing.

At least two species of a class of vertebrates that had previously failed to colonize Galápagos became established. Frogs have successfully inhabited the region of Puerto Villamil on Isabela and Puerto Ayora on Santa Cruz Island. The species in Villamil appears to be a member of the family Leptodactylidae and the species in Santa Cruz is *Scinax quinquefasciata*, a member of the family Hylidae. These families of frogs contain many species adapted for conditions drier than usually associated with frogs. Whether they will spread to the wetter highlands and what their impacts on native flora and fauna will be is hard to say. What we can say is that the combination of human activity and one of the wettest El Niños of the last 118 years has resulted in what was apparently impossible during the previous millions of years of Galápagos history – the establishment of a population of amphibians.

Introduced organisms also spread to new islands within the Archipelago, apparently as a result of the wet conditions. Smooth-billed anis established breeding populations on Genovesa and Fernandina islands. Within the last hundred years but prior to 1980, there were scattered observations of individual smooth-billed anis in Galápagos. Apparently they were either introduced or reached Galápagos on their own, but failed to colonize. Around 1980, a farmer from the highlands of Santa Cruz introduced them in the hopes that they would eat ticks from his cattle. The population remained sparse until the 1982-83 El Niño, when

they increased tremendously in numbers and spread to many new islands. Now they have spread to two islands previously free of alien vertebrates.

The rains of the 1997-98 El Niño stopped in May of 1998. A drought developed in the latter half of 1998 and the first months of 1999. Although several experienced farmers predicted that development and reduced their herds of cattle, many farmers on Santa Cruz found that they had greatly exceeded the normal carrying capacity of their farms by building up their herds during El Niño. When the drought developed, these farmers had more cattle than they could support and a poor market in which to sell them. They petitioned the Galápagos National Park Service for grazing rights within the Park and moved several hundred head onto Park land. The region where the cattle were introduced is within the reduced range of *Scalesia* and part of the tiny remnant of native highland vegetation left on Santa Cruz. The impact of the cattle is both direct and indirect. In grazing and seeking water and shade, they disturb the small native and endemic species growing under the *Scalesia* canopy, and they injure the roots of the *Scalesia*, causing trees to fall and the canopy to open. The openings they produce in the *Scalesia* stands are rapidly colonized by invasive species of introduced plants, many of which are present as seeds in the manure left by the cattle. The result is an acceleration of the spread of invasive plant species and the loss of native humid zone habitat on Santa Cruz.

*Potential consequences of stronger El Niño –  
La Niña Oscillations*

In Galápagos, several marine species appear to be on the edges of their distributions. Sea lions reach their southern extent in the islands and penguins are at their northern limits. For the last 17 years, penguins have been unable to recuperate from the mortality experienced in the 1982-83 El Niño. The developing pattern seems to be one of crashes during El Niño events and slow population growth during the subsequent intervals. The overall trend seems to be a reduction in the population that could certainly lead to extinction. The pattern in sea lions is not as well known over the long term, but observations from 1997-98 indicate that a decline could occur. At present, it is impossible to determine whether these potential declines are purely natural events in response to global climatic patterns or if they are exacerbated by the results of human activity such as introduced species or fishing.

Incidents like the colonization of Galápagos by frogs and the movement of cattle into the Park are going to increase as both the climatic oscillations and levels of human activity increase in the Galápagos. The

rate of introductions of plants to the Galápagos has increased steadily over the last twenty years as a result of human activity. If wet periods get wetter and farmers continue to exceed the carrying capacity of their farms for drought periods, the islands will experience increasing colonization and invasion by introduced species finding more suitable habitats. We predict an increasingly damaging synergy between human activity and patterns of climatic change in the short term that will present yet more challenges to the conservation biology of the Galápagos Archipelago.

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Appendix. Summary of meteorological data for Santa Cruz Island from 1965 through 1998.

**Table A1. Coastal rainfall data (mm).**

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Total	Total w/ Previous Year
1965	31.50	8.93	0.00	223.55	224.15	6.30	12.70	8.80	16.20	40.20	11.70	16.00	600.03	
1966	69.70	41.80	0.00	0.00	0.00	9.00	13.80	10.40	15.60	19.10	14.00	10.40	203.80	803.83
1967	34.60	112.00	26.90	13.80	7.90	3.80	10.60	10.90	13.25	13.70	16.50	13.30	277.25	481.05
1968	5.70	32.91	30.20	0.00	0.10	1.00	18.80	19.10	23.50	14.10	11.80	6.60	163.81	441.06
1969	23.00	16.80	249.00	68.50	31.40	16.80	12.00	3.80	18.60	3.20	11.00	15.70	469.80	633.61
1970	20.40	0.00	1.20	0.70	4.60	8.10	8.70	10.20	6.20	10.20	9.60	5.65	85.55	555.35
1971	12.30	1.50	141.90	41.20	0.40	11.50	10.00	19.70	12.30	0.50	4.70	13.50	269.50	355.05
1972	46.90	70.80	49.10	241.90	31.20	123.50	7.20	8.00	5.50	8.10	1.70	75.20	669.10	938.60
1973	399.00	11.70	10.90	0.00	1.60	0.50	0.80	6.30	6.50	8.90	8.90	14.30	469.40	1,138.50
1974	7.20	54.45	16.20	15.20	19.70	14.35	6.00	12.10	9.55	6.10	6.10	7.40	174.35	643.75
1975	2.60	335.10	417.60	108.20	0.20	6.00	4.80	16.00	8.50	14.80	3.10	12.20	929.10	1,103.45
1976	45.20	81.80	0.00	43.40	239.20	10.40	30.90	22.10	10.40	3.90	10.20	8.90	506.40	1,435.50
1977	116.30	29.00	13.80	0.00	31.80	7.00	22.50	5.20	2.50	18.60	9.40	12.30	268.40	774.80
1978	158.30	63.40	99.60	0.00	0.00	0.00	4.70	7.90	2.30	7.30	9.90	64.80	418.20	686.60
1979	44.30	31.50	0.00	44.40	1.90	12.70	8.00	3.80	14.80	3.10	0.60	4.60	169.70	587.90
1980	23.40	69.20	0.00	139.40	0.00	1.20	4.70	3.00	3.60	5.80	4.50	1.00	255.80	425.50
1981	1.50	4.40	275.30	21.00	1.00	2.10	4.50	1.20	12.20	5.90	3.20	37.50	369.80	625.60
1982	13.20	22.20	11.50	6.80	8.50	4.20	9.00	5.70	6.10	8.93	34.70	508.62	639.45	1,009.25
1983	315.90	91.90	298.90	434.20	660.20	635.50	278.20	5.40	3.10	28.30	3.00	14.10	2,768.70	3,408.15
1984	3.50	38.00	77.10	0.40	0.00	4.00	5.70	5.40	6.20	12.60	3.50	0.50	156.90	2,925.60
1985	1.80	0.00	0.00	2.70	0.00	13.80	9.80	11.00	10.80	7.60	3.20	2.90	63.60	220.50
1986	12.00	67.70	39.00	63.60	5.90	8.70	7.60	17.50	7.30	5.60	29.90	12.80	277.60	341.20
1987	124.70	379.70	310.00	170.80	191.20	3.90	20.10	22.30	14.80	5.30	5.00	5.80	1,253.60	1,531.20
1988	14.30	8.30	0.00	0.00	2.00	1.60	9.80	7.40	13.90	9.90	7.60	3.70	78.50	1,332.10
1989	10.60	7.10	0.20	2.10	11.20	1.20	8.90	13.70	5.40	9.00	9.90	3.20	82.50	161.00
1990	8.90	176.20	17.40	1.00	4.30	6.90	4.90	8.90	14.30	7.60	18.10	9.00	277.50	360.00
1991	17.50	118.10	256.20	0.00	0.80	12.30	17.40	8.90	13.40	15.70	15.70	27.30	503.30	780.80
1992	105.70	109.30	113.80	313.60	154.40	8.70	3.10	14.60	7.70	10.50	14.10	0.80	856.30	1,359.60
1993	61.60	144.40	162.20	65.60	230.00	9.90	17.20	22.00	3.91	8.35	9.15	12.95	747.26	1,603.56
1994	33.20	7.05	0.00	0.00	1.50	6.50	11.00	6.70	10.10	1.90	2.90	106.31	187.16	934.42
1995	183.20	8.50	40.00	0.30	1.30	4.10	13.60	9.90	25.70	15.70	4.80	9.70	316.80	503.96
1996	53.60	43.80	20.50	0.00	0.30	4.90	13.50	14.60	11.00	6.00	6.60	11.80	186.60	503.40
1997	4.30	97.80	253.20	401.20	137.20	247.60	24.30	12.10	4.90	7.90	146.90	317.80	1,655.20	1,841.80
1998	396.30	342.90	221.30	448.30	245.60	53.50	5.10	15.90	3.60	3.10	13.30	3.50	1,752.40	3,407.60
Mean	70.65	77.30	92.74	84.47	66.16	37.10	18.82	10.90	10.11	10.22	13.68	40.30	532.45	1,025.89
Median	27.45	42.80	28.55	14.50	4.45	6.95	9.80	10.05	9.83	8.23	9.28	12.00	297.20	774.80
Standard Deviation	105.75	97.94	119.06	134.23	133.78	115.26	46.31	5.82	5.79	7.79	24.66	100.06	572.88	830.73
Coefficient of Variation	149.67	126.70	128.39	158.91	202.20	310.65	246.06	53.36	57.29	76.22	180.19	248.31	107.59	80.98



**Table A2. Upper Transition Zone (Bellavista) rainfall data (mm).**

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept.	Oct	Nov	Dec	Total	Total w/ Previous Year
1987							51.80	96.10	88.80	33.20	67.20	76.90	414.00	
1988	33.70	39.10	0.00	0.00	3.80	4.00	48.00	59.80	93.00	77.20	75.40	13.50	447.50	861.50
1989	38.20	81.80	6.80	8.70	29.30	19.50	48.30	80.80	60.00	83.20	66.90	14.80	538.30	985.80
1990	24.10	220.60	36.40	9.60	20.10	44.50	44.60	72.00	75.30	78.80	131.00	33.40	790.40	1328.70
1991	39.50	372.60	240.40	0.00	14.20	53.30	88.40	61.10	73.50	105.50	89.40	155.10	1293.00	2083.40
1992	290.40	259.10	106.20	469.30	297.00	22.20	27.10	83.80	51.20	89.50	33.80	15.60	1745.20	3038.20
1993	24.00	208.70	173.70	117.60	107.70	77.80	111.00	42.60	22.90	60.80	65.10	54.70	1066.60	2811.80
1994	70.50	146.20	0.00	0.00	5.50	39.60	72.30	75.70	68.30	23.50	20.00	277.90	799.50	1866.10
1995	374.10	18.70	20.00	0.90	2.50	18.50	50.30	71.00	112.20	64.00	36.00	40.70	808.90	1608.40
1996	52.70	60.50	110.10	0.40	6.20	21.60	77.00	74.50	92.60	50.00	60.80	47.60	654.00	1462.90
1997	9.00	155.10	291.80	390.50	321.40	172.40	130.20	67.10	42.10	101.20	347.30	619.90	2648.00	3302.00
1998	347.15	388.40	318.40	528.00	302.70	104.10	16.60	41.86	11.70	15.50	27.10	9.10	2110.61	4758.61
Mean	118.49	177.35	118.53	138.64	100.95	48.13	63.80	68.86	65.97	65.20	85.00	113.27	1109.67	2191.58
Median	39.50	155.10	106.20	8.70	20.10	30.90	51.05	71.50	70.90	70.60	66.00	44.15	804.20	1866.10
Standard Deviation	142.66	126.78	120.47	213.10	135.72	49.46	33.37	15.85	29.96	29.62	88.04	177.43	710.49	1178.15
Coefficient of Variation	120.40	71.49	101.64	153.71	134.45	102.77	52.30	23.02	45.41	45.42	103.57	156.64	64.03	53.76

**Table A3. Coastal air temperature data (°C, 1200h).**

Year	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.	Mean	
1965	26.48	28.59	30.01	28.89	27.86	26.85	25.45	24.65	24.25	24.44	25.2	26.17	26.57	
1966	27.95	28.9	28.45	27.55	25.68	24.21	23.37	22.14	22.2	23	23.53	24.95	25.16	
1967	26.76	28.02	29.62	28.5	27.24	24.78	22.85	22.22	21.5	22.24	23.47	23.71	25.08	
1968	26.58	27.9	28.3	27.08	25.24	23.91	23.39	24.21	24.13	24.35	24.6	26.1	25.48	
1969	27.27	28.89	29.87	29.45	28.67	27.41	24.69	24.17	24.14	25.68	26.16	26.88	26.94	
1970	27.73	28.73	29.01	27.9	26.37	24.11	21.76	21.67	22.24	22.97	24.16	24.99	25.14	
1971	26.85	27.89	28.13	29.29	26.07	24.56	23.76	22.31	22.72	24.02	24.9	25.1	25.47	
1972	26.89	28.93	30.05	29.12	27.85	26.99	26.76	26.59	25.7	25.96	26.82	27.62	27.44	
1973	28.47	30.05	29.95	27.47	26.48	24.46	23.26	22.61	22.68	22.89	24.22	25.41	25.66	
1974	26.92	29.29	28.95	29.7	27.72	25.58	24.09	23.52	23.38	23.04	23.71	24.08	25.83	
1975	26.53	27.43	29.14	28.61	26.19	24.67	23.59	22.43	22.06	22.07	22.42	24	24.93	
1976	27.06	28.92	30.06	29.74	28.35	27.29	26.46	25.95	24.89	25.37	25.89	26.72	27.22	
1977	28.59	30	30.11	29	27.3	26.11	24.22	22.28	22.17	23.1	24.51	25.41	26.07	
1978	26.67	28	27.57	27.26	25.91	23.18	22.89	21.74	21.56	22.55	23.9	25.12	24.7	
1979	27.38	27.86	28.89	28.4	26.7	25.07	24.25	23.3	23.86	23.88	24.79	25.11	25.79	
1980	27.06	28.26	29.14	28.92	26.82	25.17	23.87	22.77	22.33	23	23.97	24.9	25.52	
1981	25.98	27.74	28.33	27.7	26.65	24.91	23.21	22.51	21.97	22.7	23.57	25.43	25.06	
1982	26.64	28.23	27.97	27.19	26.45	25.1	24.37	24.07	24.87	25.78	27.21	27.68	26.3	
1983	29.4	30.12	30.11	29.79	28.79	28.34	27.64	26.25	24.68	24.66	24.7	25.61	27.51	
1984	26.63	27.36	28.76	27.1	25.61	23.88	22.66	22.21	22.42	22.74	24.25	25.34	24.91	
1985	26.03	26.7	27.75	27.5	24.52	24.22	22.43	21.37	21.51	22.2	23.84	24.63	24.39	
1986	26.94	28.59	29.24	27.63	26.43	24.53	23.88	23.41	23.24	23.8	24.64	25.84	25.68	
1987	27.59	28.61	29.27	29.36	27.7	25.96	24.87	24.39	24.74	25.1	25.62	26.25	26.62	
1988	27.43	28.3	28.37	26.26	25.49	23.22	21.64	20.96	21.65	22.01	22.92	24.61	24.4	
1989	26.53	28.89	28.51	28.77	26.35	24.38	23.26	22.9	22.09	23.07	23.96	24.59	25.27	
1990	26.65	28.38	29.14	28.49	26.95	24.92	23.36	22.71	22.96	22.6	23.47	25.02	25.39	
1991	26.69	28.46	28.87	27.22	27.48	25.76	24.44	23.7	23.22	23.85	24.57	26.09	25.86	
1992	26.93	29.03	29.86	29.01	27.93	25.38	23.73	22.59	22.31	22.87	23.79	25.37	25.73	
1993	26.93	28.48	29.02	29.22	27.85	26.32	24.8	24.05	24.06	23.91	24.79	26.01	26.29	
1994	27.63	28.7	27.97	25.99	26.01	24.57	24	22.21	22.33	23.96	24.83	26.02	25.35	
1995	28.03	29.35	29.2	26.07	25.89	25	23.38	22.24	22.57	22.99	23.72	24.74	25.27	
1996	26.6	28.36	28.7	26.47	25.33	23.79	22.55	21.85	21.4	22.57	23.01	23.54	24.51	
1997	26.18	28.29	29.04	28.77	28.13	27.82	27.5	27.19	27.24	26.98	27.62	28.64	27.78	
1998	30.27	30.32	30.31	29.4	28.6	27.47	25.42	24.37	23.92	23.96	24.57	25.3	26.99	
Mean	27.18	28.58	29.05	28.20	26.84	25.29	24.05	23.28	23.15	23.66	24.51	25.50		
Median	26.92	28.53	29.03	28.50	26.68	24.96	23.81	22.74	22.70	23.08	24.38	25.35		
Standard Deviation	0.922	0.8	0.757	1.121	1.102	1.343	1.442	1.522	1.373	1.246	1.177	1.113		
Coefficient of Variation	3.392	2.8	2.605	3.976	4.105	5.311	5.997	6.538	5.932	5.268	4.802	4.364		

**Table A4. Upper Transition Zone (Bellavista) temperature data (°C, 1200h).**

Year	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.	Mean
1987						24.32	23.70	22.84	23.96	24.21	24.02	25.10	24.02
1988	26.57	28.65	30.03	29.57	26.94	24.32	21.49	20.54	20.92	21.38	22.13	23.86	24.70
1989	26.93	29.40	31.05	29.39	25.92	24.05	23.21	22.69	21.43	22.21	23.23	23.87	25.28
1990	25.71	27.77	29.57	29.62	26.71	25.03	23.33	21.98	22.41	21.63	22.12	24.01	24.99
1991	26.36	28.21	28.81	28.80	27.23	24.73	23.22	22.71	22.00	22.61	23.62	24.60	25.24
1992	25.87	27.95	29.56	28.23	27.78	25.56	23.17	21.83	21.39	21.98	22.87	24.96	25.09
1993	27.03	27.80	29.50	29.53	26.73	25.33	23.42	23.15	23.55	22.79	23.41	24.61	25.57
1994	26.87	28.36	30.33	29.18	26.45	23.99	23.17	21.04	21.38	23.19	24.03	24.62	25.22
1995	26.53	29.52	30.21	27.83	26.43	24.74	22.19	20.86	20.89	21.50	22.93	23.85	24.79
1996	26.13	28.12	28.88	28.06	26.60	22.93	21.63	20.85	20.19	22.08	22.09	23.01	24.21
1997	25.93	27.90	28.28	28.66	27.20	27.35	26.02	25.95	26.11	25.25	26.00	27.25	26.82
1998	29.17	29.32	29.79	28.75	27.85	26.60	24.90	24.34	23.59	23.80	24.45	25.18	26.48
Mean	26.64	28.45	29.64	28.87	26.89	24.91	23.29	22.40	22.32	22.72	23.41	24.58	
Median	26.53	28.21	29.57	28.80	26.73	24.73	23.22	22.34	21.71	22.41	23.32	24.60	
Standard Deviation	0.95	0.67	0.78	0.64	0.58	1.19	1.26	1.59	1.69	1.20	1.13	1.05	
Coefficient of Variation	3.57	2.34	2.63	2.21	2.17	4.79	5.41	7.11	7.56	5.26	4.85	4.29	

**Table A5. Sea temperature data (°C, 0600h).**

Year	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.	Mean
1965	23.67	25.77	26.39	26.72	26.89	25.45	23.58	23.03	23.05	23.18	23.81	24.39	24.66
1966	25.93	25.95	24.44	23.62	22.54	22.17	21.75	20.92	21.54	21.57	22.41	22.37	22.93
1967	24.26	24.84	24.58	24.39	23.24	22.94	21.79	20.82	20.00	21.25	22.05	21.93	22.67
1968	22.96	24.13	23.49	23.24	22.45	21.43	22.26	22.65	23.02	23.11	23.08	23.79	22.97
1969	24.48	25.59	27.22	27.56	26.80	25.56	22.59	21.99	22.29	23.31	23.66	24.65	24.64
1970	24.75	24.63	24.04	24.34	22.95	21.02	19.98	19.95	20.83	21.27	22.72	22.43	22.41
1971	23.66	24.58	25.52	26.35	24.04	22.93	22.46	21.61	21.32	22.50	22.93	22.40	23.36
1972	24.12	25.87	26.06	27.71	26.31	24.75	24.27	23.97	23.52	23.52	24.13	25.61	24.99
1973	26.99	25.96	25.33	23.46	21.87	20.71	20.83	20.43	20.61	20.52	21.71	22.37	22.57
1974	23.09	25.13	24.28	25.82	25.02	23.89	21.95	21.03	21.17	20.92	21.34	20.78	22.87
1975	22.96	25.55	26.19	26.36	23.53	22.30	21.66	20.94	20.70	20.40	20.53	21.34	22.71
1976	23.30	24.20	25.01	26.12	26.50	25.41	24.61	23.98	22.81	22.63	23.62	24.25	24.37
1977	25.62	25.48	24.53	24.12	23.76	22.90	21.94	20.85	20.54	22.00	22.89	23.59	23.18
1978	25.06	25.96	25.42	23.76	22.93	20.93	21.32	20.48	20.14	21.55	22.25	23.23	22.75
1979	25.37	25.26	25.24	26.59	24.46	23.36	22.55	21.93	22.47	22.46	23.16	23.41	23.85
1980	24.70	25.43	24.96	25.43	24.38	22.93	22.45	21.14	20.99	21.62	22.61	22.57	23.27
1981	23.11	24.46	24.87	25.48	24.59	23.28	22.08	20.26	21.10	21.27	21.51	23.31	22.94
1982	24.28	25.39	25.40	24.95	25.29	24.24	23.82	23.17	23.40	24.18	25.94	26.92	24.75
1983	27.57	27.89	28.56	28.54	27.94	27.50	26.75	24.31	22.28	22.41	22.44	23.22	25.78
1984				24.82	23.13	22.09	21.98	21.47	21.76	22.21	22.62	23.16	22.58
1985	23.66	23.58	24.11	25.02	22.65	22.48	22.34	21.43	21.13	21.44	22.39	22.70	22.74
1986	24.14	25.62	25.47	24.79	24.75	22.96	22.81	22.55	21.84	22.25	23.47	24.15	23.73
1987	25.84	27.37	27.48	27.95	26.59	24.42	22.89	23.00	23.31	23.09	23.60	23.89	24.95
1988	24.15	24.56	24.54	22.68	21.58	19.96	18.96	19.83	20.98	20.25	21.60	22.09	21.77
1989	23.41	25.23	24.52	25.82	24.59	23.03	21.81	22.16	21.50	21.83	22.08	22.22	23.18
1990	23.94	26.25	25.07	26.16	25.22	23.31	21.78	21.39	21.47	21.43	23.01	23.25	23.52
1991	23.85	26.37	26.82	23.44	25.21	24.69	23.50	22.35	22.28	22.55	23.23	24.43	24.06
1992	25.81	27.52	27.78	28.38	26.82	23.65	21.65	21.45	21.11	21.53	22.03	23.19	24.24
1993	24.15	26.14	26.37	27.40	26.52	24.88	23.47	21.64	21.66	22.10	22.96	23.32	24.22
1994	24.61	25.20	23.51	22.32	22.50	23.13	22.16	21.35	21.08	22.11	23.51	24.56	23.00
1995	26.28	25.78	25.30	22.43	22.44	22.11	21.70	20.69	21.20	21.56	22.13	21.97	22.80
1996	23.44	24.84	25.59	23.22	22.37	21.35	21.24	20.71	20.09	20.97	21.45	21.27	22.21
1997	23.05	25.36	26.71	27.13	27.03	26.71	26.48	25.91	25.83	25.98	26.65	27.75	26.21
1998	27.87	27.85	28.47	28.46	26.89	25.80	23.09	21.99	20.98	21.05	22.45	21.63	24.71
Mean	24.55	25.57	25.55	25.43	24.52	23.36	22.49	21.81	21.71	22.06	22.82	23.30	
Median	24.15	25.48	25.33	25.46	24.52	23.08	22.21	21.46	21.40	21.91	22.67	23.22	
Standard Deviation	1.32	1.02	1.32	1.84	1.81	1.75	1.53	1.35	1.21	1.15	1.20	1.50	
Coefficient of Variation	5.39	4.00	5.15	7.23	7.37	7.50	6.79	6.19	5.57	5.23	5.25	6.43	

Table A6. Sea temperature anomalies (°C,  $X_i - \bar{X}_{1965-1998}$ ).

Year	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.	Mean
1965	0.10	2.19	2.81	3.14	3.31	1.87	0.00	-0.54	-0.53	-0.39	0.23	0.82	1.08
1966	2.35	2.38	0.86	0.04	-1.04	-1.41	-1.83	-2.66	-2.03	-2.01	-1.17	-1.21	-0.64
1967	0.69	1.26	1.00	0.82	-0.34	-0.63	-1.79	-2.75	-3.58	-2.33	-1.53	-1.65	-0.90
1968	-0.62	0.55	-0.09	-0.33	-1.13	-2.14	-1.31	-0.93	-0.56	-0.47	-0.50	0.21	-0.61
1969	0.90	2.02	3.65	3.99	3.22	1.98	-0.99	-1.59	-1.28	-0.27	0.08	1.07	1.06
1970	1.18	1.06	0.46	0.77	-0.63	-2.55	-3.60	-3.62	-2.75	-2.31	-0.86	-1.14	-1.17
1971	0.08	1.01	1.94	2.77	0.46	-0.65	-1.12	-1.96	-2.26	-1.08	-0.65	-1.18	-0.22
1972	0.54	2.29	2.49	4.13	2.73	1.17	0.69	0.39	-0.06	-0.06	0.55	2.03	1.41
1973	3.42	2.39	1.76	-0.12	-1.71	-2.87	-2.75	-3.15	-2.96	-3.06	-1.86	-1.21	-1.01
1974	-0.49	1.55	0.71	2.25	1.45	0.31	-1.63	-2.55	-2.41	-2.65	-2.24	-2.80	-0.71
1975	-0.61	1.98	2.61	2.79	-0.05	-1.28	-1.92	-2.64	-2.88	-3.18	-3.05	-2.24	-0.87
1976	-0.28	0.62	1.43	2.54	2.92	1.83	1.03	0.40	-0.77	-0.94	0.04	0.67	0.79
1977	2.04	1.90	0.95	0.54	0.18	-0.67	-1.64	-2.73	-3.04	-1.58	-0.68	0.01	-0.39
1978	1.49	2.38	1.84	0.18	-0.65	-2.64	-2.25	-3.09	-3.44	-2.03	-1.33	-0.35	-0.83
1979	1.79	1.69	1.66	3.01	0.88	-0.21	-1.03	-1.65	-1.11	-1.12	-0.41	-0.17	0.28
1980	1.12	1.86	1.38	1.85	0.80	-0.65	-1.13	-2.44	-2.58	-1.95	-0.96	-1.00	-0.31
1981	-0.47	0.88	1.29	1.91	1.01	-0.29	-1.50	-3.32	-2.48	-2.31	-2.07	-0.27	-0.63
1982	0.70	1.81	1.82	1.37	1.71	0.67	0.24	-0.41	-0.18	0.60	2.36	3.35	1.17
1983	3.99	4.32	4.98	4.97	4.36	3.93	3.17	0.73	-1.29	-1.17	-1.14	-0.36	2.21
1984				1.25	-0.45	-1.49	-1.60	-2.11	-1.82	-1.36	-0.96	-0.42	-1.00
1985	0.08	0.00	0.53	1.45	-0.93	-1.10	-1.24	-2.14	-2.44	-2.14	-1.19	-0.88	-0.83
1986	0.56	2.04	1.89	1.21	1.18	-0.62	-0.77	-1.03	-1.74	-1.33	-0.10	0.57	0.16
1987	2.26	3.79	3.90	4.37	3.01	0.84	-0.69	-0.57	-0.26	-0.48	0.02	0.32	1.38
1988	0.57	0.99	0.96	-0.90	-2.00	-3.62	-4.61	-3.75	-2.59	-3.33	-1.97	-1.48	-1.81
1989	-0.17	1.65	0.95	2.25	1.01	-0.55	-1.77	-1.42	-2.07	-1.75	-1.50	-1.36	-0.39
1990	0.36	2.67	1.49	2.59	1.64	-0.27	-1.79	-2.18	-2.11	-2.15	-0.57	-0.33	-0.05
1991	0.28	2.79	3.24	-0.14	1.64	1.12	-0.08	-1.23	-1.29	-1.03	-0.35	0.85	0.48
1992	2.23	3.94	4.21	4.81	3.25	0.07	-1.93	-2.13	-2.47	-2.05	-1.55	-0.39	0.67
1993	0.57	2.56	2.79	3.82	2.95	1.30	-0.10	-1.94	-1.92	-1.48	-0.61	-0.26	0.64
1994	1.03	1.63	-0.07	-1.25	-1.08	-0.45	-1.42	-2.23	-2.50	-1.46	-0.07	0.99	-0.57
1995	2.70	2.20	1.72	-1.15	-1.14	-1.47	-1.87	-2.89	-2.37	-2.02	-1.44	-1.60	-0.78
1996	-0.14	1.27	2.01	-0.36	-1.20	-2.23	-2.34	-2.87	-3.49	-2.60	-2.12	-2.31	-1.37
1997	-0.53	1.78	3.13	3.55	3.45	3.13	2.90	2.33	2.25	2.40	3.07	4.17	2.64
1998	4.29	4.27	4.89	4.88	3.31	2.22	-0.48	-1.59	-2.59	-2.53	-1.13	-1.94	1.13
Mean	0.97	1.99	1.98	1.85	0.95	-0.22	-1.09	-1.77	-1.87	-1.52	-0.75	-0.28	
Median	0.57	1.90	1.76	1.88	0.95	-0.50	-1.37	-2.12	-2.18	-1.66	-0.91	-0.35	



## SANTIAGO'S PIGS AND ISABELA'S GOATS: EL NIÑO'S IMPLICATIONS FOR MANAGEMENT AND THE ENVIRONMENT

**Karl Campbell**

Above average levels of rainfall during the 1997-98 El Niño provided an increase in available resources for both feral and native terrestrial animals, by promoting an increase in vegetation biomass and providing surface water, which is scarce in normal years. This affected pig and goat populations in quite different ways and had implications for their habitat and for hunting success.

On Santiago Island, the last few years have seen an intensive and consistent effort that will soon achieve the eradication of the pigs. However, since pigs are limited in part by the availability of surface water, the abundant rains of El Niño allowed them to expand their range, which had been diminishing due to hunting pressure. In addition, increased vegetation density caused by the rains reduced hunter success, as large areas became impenetrable to hunters and dogs alike. As a result, pig populations recuperated somewhat during El Niño. During the months following El Niño, water points began drying up and vegetation began dying off. Pigs were forced to concentrate around ever-diminishing permanent water points. The movement of hunters and dogs then became less constrained by vegetation and the kill rate increased dramatically, especially in the five months following the end of the rains (June – October). Expected post-El Niño drought conditions (La Niña) should speed the eradication of pigs on Santiago.

On nearby Alcedo Volcano, on Isabela Island, these same drought conditions threaten to provoke destruction

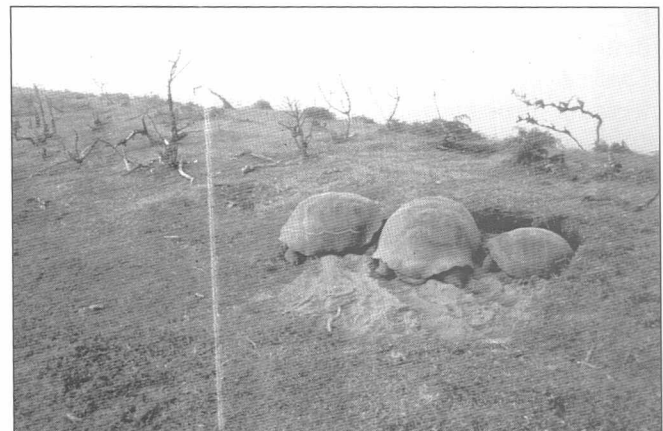
by goats of critically important natural habitat, so preventive measures are planned. On Alcedo, El Niño rains brought about a vigorous vegetation growth, as they did on Santiago. Widespread availability of vegetation allowed feral goats to disperse over a wider area, thus reducing direct browsing pressure on Alcedo's southern rim. As a result, vegetation biomass may have stabilized or increased during El Niño in this particular area. However, the overall increase in vegetation is likely also to have assisted in the goats' reproductive success, which will continue even after vegetative production slows, magnifying the detrimental impacts of the goats. The predicted La Niña is expected to produce drought conditions that will concentrate goat activity on the rim. Regularly scheduled control hunts will aim to limit goat damage to acceptable levels until the eradication campaign for goats on northern Isabela is fully funded and ready to be implemented. El Niño may have temporarily slowed the degradation of habitat on Alcedo, but the goat menace is as potent as ever - their eradication is essential for the survival of the ecosystem.

For the Project Isabela team, charged with the management of both the Santiago pig and the Isabela goat eradication campaigns, El Niño has been a mixed blessing, as will the expected drought of La Niña.

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*Giant tortoises gathering in drizzle fog drip areas on caldera rim during garua season. Photograph by Tui De Roy.*



*Giant tortoises huddling on barren caldera rim ravaged by new goat invasion, fog drip trees destroyed. Photograph by Tui De Roy.*

## EFFECTS OF THE 1997-98 EL NIÑO EVENT ON THE VEGETATION OF GALÁPAGOS

Alan Tye and Iván Aldaz

### INTRODUCTION

During the last large El Niño event, in 1982–83, heavy rain fell on Galápagos for nine months, forming rivers and eroding channels in many places, including normally arid areas. The vegetational changes that took place during that El Niño event are summarized by Hamann (1985).

Similar changes occurred during the most recent El Niño, which began in early 1997 with a heavier-than-normal rainy season and continued to the end of the wet season in 1998. During 1997, there was no garúa season, merely a drier period about September–October, and the vegetation did not dry up as in normal years. In some areas with friable soils, such as southern Santa Cruz Island and Alcedo Volcano on Isabela Island, the heavy rains produced powerful temporary watercourses, which eroded deep channels and removed all surface vegetation, including large trees.

### EFFECTS ON THE VEGETATION OF THE SEMI-ARID ZONES

#### *Herbaceous vegetation*

In the Littoral, Arid, and Transition zones of the larger islands and throughout the lower islands, the general appearance during July–December 1997 was much greener than is usual for this normally dry part of the year. The herbaceous understorey layer, dominated by grasses, annual herbs, and creepers, was unusually dense. Among herbaceous species, *Mentzelia aspera* and *Cassia tora* became extremely common, each in places forming dense monospecific stands of height about 1–1.5 m. In many places, creepers (both native and introduced species) covered the bushes and trees in a dense carpet. Among the native species of creeper, *Passiflora foetida* did particularly well. *Rhynchosia minima* also became very abundant, apparently throughout the archipelago (including Genovesa, Santiago, San Cristóbal, Santa Cruz, and Isabela islands, among others), as in 1982–83 (Hamann 1985). Of the introduced species, *Momordica charantia* and *Cucumis dipsaceus* became much more widely distributed than in normal years. On Floreana Island, *Cucumis* was found covering huge areas of shrubland and woodland in the Arid and Transition zones. It has since died back, and it is unclear whether El Niño has allowed it to extend its distribution or whether it was already widely distrib-

uted but was formerly, in normal years, much less conspicuous. *Cucumis* was first recorded on Española Island during the 1982–83 El Niño. It became very common again on that island during the recent event. *Momordica* became a very obvious component of the Arid Zone vegetation on several islands. In all of these cases, it is hard to know whether this apparent change represents a real extension of distribution, or just a temporary increase in abundance in areas where the plants were already present.

#### *Cactaceae*

The Cactaceae both benefitted and suffered from the effects of El Niño. Their rate of growth and flower production were greater, this being especially obvious in species of *Opuntia*, but they absorbed so much water that many larger *Opuntia* trees fell over under their own weight, as happened in the previous El Niño (Hamann 1985, Luong and Toro 1985). The plants have a relatively weak and shallow root system, which is not capable of supporting such a weight increase, combined with the stronger winds that are experienced during El Niño. Despite this mortality of adults, in many places, regeneration of young plants both by seed and vegetatively, was great during the Niño period. Large numbers of young cacti were seen in many places in the months following El Niño. These include not only individuals growing from seed that germinated during El Niño, but, judging from their size, there are also many young plants that had germinated in preceding years. These may have experienced a sudden growth spurt, having been “waiting” for the favourable conditions for growth that were provided by El Niño. In contrast to the reports for the 1982–83 El Niño (Hamann 1985), the *Opuntia* flowered well twice: at the beginning of the event in 1997, and again at the beginning of the rainy season following El Niño, in early 1999.

#### *Lowland Scalesia species*

Effects on the lowland species of *Scalesia* were mixed. Although no formal monitoring was carried out, these species are so conspicuous that effects on them are comparatively easy to judge. In addition, two projects begun during El Niño allowed us to collect some data on their populations. One project is to monitor selected rare species for growth and reproduction, and the other intends to bring up to date our knowledge of the status and distribution of endemic plant

species of Galapagos. Both include *Scalesia* species among their subjects. These observations revealed that during El Niño many adult plants of lowland zone *Scalesia* species died, perhaps because of root rot or temporary flooding. One or both of these probably caused the death of plants of *Scalesia helleri* in the demonstration gardens at CDRS, where nearly all of the plants that had been cultivated over the previous three years died. Mortality was also observed in adults of this species in wild populations on southern Santa Cruz, as was the case among older adults of *Scalesia crockeri* (northern Santa Cruz), *S. incisa*, and *S. divisa* (both of San Cristobal). On the other hand, all of these species showed dramatically increased regeneration, with virtually every adult of *S. helleri*, *S. incisa*, and *S. divisa* surrounded by a circle of young plants. In the case of *S. crockeri*, the population on the south coast of Baltra Island increased enormously, spreading from a few isolated patches, to a more or less continuous fringe along the coastal cliff. Similarly, the growth of *Scalesia helleri* on Santa Fe Island has been impressive, as in 1982–83 (Hamann 1985). It is hard to generalize from one group of plants to another, but it seems likely that many plants that share habitat requirements and growth characteristics with the lowland *Scalesia* species would have been similarly affected.

Effects on the rarest plant of Galápagos, *Scalesia atractyloides*, were unclear. The species was believed extinct until, in 1995, a population of *S. a. darwinii* was discovered, consisting of five adult plants growing on the vertical wall of a crater. Two of the five died in early 1997 from unknown causes; they might simply have been old, or heavy rain might have affected them adversely. The crater was enclosed by a fence in December 1997, but the other three adults died at some time during mid-1998. During 1997, several seedlings were found below the adult plants. Although most of these disappeared (probably eaten by goats) during the year, a few survived until the fence was constructed. Unfortunately, two goats entered the crater through a gap in the fence (now closed) and most of the seedlings disappeared. To date, two remain. A drought due to La Niña might reduce the chance of more plants growing from seed during 1999. In November 1998, the other variety of the species, *S. a. atractyloides*, was rediscovered, after having not been seen since the 1980s, at a site on the west coast of Santiago. Only two adults are still alive at the site, and no seedlings have been seen. Again, although the site has now been fenced (in December 1998), regeneration from seed could be delayed by a Niña drought.

#### *Growth and phenology*

Many species developed leaves much larger than in normal years, in some cases to such an extent that they

appeared to be a different species. This was true of many species of shrub and tree of the Arid and Transition zones, including *Cordia lutea*, *Bursera graveolens*, *Piscidia carthagenensis*, *Croton scouleri*, and *Cryptocarpus pyriformis*. In some cases, flowers and inflorescences were also larger than normal. Many bushes grew higher than normal, including especially *Cryptocarpus*. There was also a greater rate of growth in height and trunk diameter of many shrub and tree species (see data from Alcedo in Aldaz and Tye, this issue). *Bursera graveolens*, which is normally leafless for most of the year, retained its leaves for longer, and individual trees lost their usual synchrony in the timing of leaf production and leaf fall.

#### *New records*

Few new records of introductions to islands were made during the 1997–98 El Niño, although it is probable that some have so far gone unnoticed. The new island records that were reported are unlikely to have been the result of spread facilitated by El Niño itself.

### EFFECTS ON THE VEGETATION OF THE HUMID ZONES

#### *Vegetation communities*

In the higher parts of the larger islands, the ferns, herbs, grasses, and creepers grew tremendously, forming dense, impenetrable masses. Both native and introduced species flourished. Certain introduced species, including *Rubus niveus*, *Lantana camara*, and *Ricinus communis*, spread noticeably during the extended wet period.

Regeneration of native species was good in areas of the highlands that are badly overgrazed by goats and other feral ungulates. On both Alcedo Volcano and Santiago Island, the areas of the highlands that have been converted in recent years to open pasture or bare ground were covered with denser growth of grasses. Among the grass, regeneration of shrub and tree species was excellent. There seem to have been two reasons for this. The goats and other animals had largely dispersed to the lower parts of the islands, where the green vegetation was unusually succulent. Combined with this, the heavy rains led to increased germination and growth of young plants or resprouts. In the highlands of Santiago, the grassy areas, which were formerly mixed *Scalesia pedunculata* – *Zanthoxylum fagara* – *Tournefortia rufosericea* forest, developed abundant regeneration, especially of *Tournefortia*. Unfortunately, as El Niño ended, the goats moved back to the highlands and have already, within months, destroyed much of this new growth. In some species, this



may have depleted a precious seedbank without contributing to the production of replacement seeds. Regeneration of *Scalesia pedunculata* on Santiago was mainly limited to the small patches with remaining adult trees, reflecting its relatively short-distance seed dispersal mechanism (Hamann 1979). Many young plants, up to 2.5 m height, were found in such patches. Unfortunately, as the goats moved back to the highlands, these saplings were their prime targets, and most were immediately killed by having their bark eaten.

Further observations from the humid zones of Alcedo are presented by Aldaz and Tye (this issue).

### Miconia robinsoniana

Effects on certain vegetation communities were marked. *Miconia robinsoniana*, the dominant shrub of the Miconia Zone on Santa Cruz, grew very well during El Niño, with bushes reaching over 3 m in height. Regeneration was good in areas where the species had been rare in preceding years and which had been dominated recently by a fern-sedge community. Regeneration was similarly good in areas heavily invaded by *Cinchona succirubra*, where the *Cinchona* was cleared by the Galapagos National Park Service (GNPS), such as on the outer slopes of Media Luna. Unfortunately, the *Cinchona* also did well during El Niño, and the density of young plants is now very high, across the majority of the area of the Miconia and Fern-sedge zones.

### Scalesia pedunculata

The forests of *Scalesia pedunculata* in the highlands of Santa Cruz suffered a mass dieback during and after El Niño of 1982–83. Causes were thought to be root rot and high winds during El Niño rains, combined with the succeeding La Niña drought (Hamann 1985). The dieback resulted in strikingly even-aged stands of the species, which date from the subsequent regeneration. This phenomenon has not been repeated during the current event. Some wind-throw of adult trees was experienced, but no mass die-off of entire stands. Wind-throw also affected other trees in the highlands, including *Cinchona succirubra*, where many adult trees

were seen with branches torn off, although relatively few trees were blown over. It remains to be seen whether a Niña drought continuing through the rainy season of 1999 will contribute to increased mortality of the *Scalesia*, but so far the effects do not seem as severe as in 1982–83. Hamann (1985) suggested that the normal lifespan of *Scalesia pedunculata* is about 15 years. If that is true, then the majority of the trees in the highland forests, at least on Santa Cruz, are near the end of their lives, since they germinated about 1982–84. Mass dieback now might be facilitated by the poor resistance of such older trees to unfavorable environmental conditions such as drought. Species undergoing periodic dieback and regeneration cycles, such as *Scalesia pedunculata* are vulnerable to invasion by species with a more continuous growth and regeneration pattern. Invasive species such as *Cinchona succirubra* and *Pennisetum purpureum* have become much more common since the 1982–83 event. A worry now is that a mass dieback of *Scalesia pedunculata* could be followed by invasion of its habitat by aggressive alien species of plant, which could prevent the regeneration of the *Scalesia* forests and thereby replace them. It remains to be seen whether this will take place in the coming year.

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## EFFECTS OF THE 1997-98 EL NIÑO EVENT ON THE VEGETATION OF ALCEDO VOLCANO, ISABELA ISLAND

Iván Aldaz and Alan Tye

### INTRODUCTION

On the majority of the islands, islets, and even rocks that form the Galápagos Archipelago, El Niño caused changes in the native plant communities of Galápagos (see also article by A. Tye and I. Aldaz in this issue). In this article, we discuss the effects produced by the intense and constant rainfall on the vegetation of Alcedo Volcano, Isabela Island, by means of studies carried out before and after El Niño.

### METHODS

Alcedo is one of the five active volcanoes comprising Isabela Island. At present it is a site with enormous ecological problems caused primarily by goats (*Capra hircus*), whose numbers were estimated before El Niño to be between 75,000 and 100,000 (Cayot 1997). In November 1995, a vegetation monitoring system was begun on Alcedo, whose objective is to evaluate the recovery of the vegetation during campaigns to eradicate introduced animals. Fourteen quadrats of 900 m<sup>2</sup> were established in the area of greatest impact, that is, on the

southern portion of the volcano. In addition, one year later, four quadrats of 400 m<sup>2</sup> were set up to monitor the status of *Darwiniothamnus tenuifolius* and *Scalesia microcephala* (Figure 1). Monitoring was carried every six months, alternating between the garúa season (light mists, from May to October) and the season with intense rainfall, from November to April. Basically, the monitoring consists of making a floristic inventory, measuring the plant cover, and measuring the diameter at breast-height (DBH) of trees and bushes. The last variable is usually measured every 12 months. More details on methodology of vegetation monitoring can be found in the monitoring manual of Mauchamp (1996).

### RESULTS

The results from the monitoring program allow an evaluation of the effects of El Niño on the vegetation of Alcedo Volcano, comparing the data obtained before the phenomenon (monitoring between November 1995 and June 1997), during El Niño (monitoring in November 1997 and April 1998), and after it (monitoring in October 1998). In this article we present a preliminary analysis that gives a general idea of the changes in the floristic composition on Alcedo during El Niño. The precipitation data are only indicative, since the measurements are from the meteorological station at the Charles Darwin Research Station on Santa Cruz Island. It should be mentioned that the quantity of millimeters of rain is that which accumulated between each date. A fuller analysis will be published following the acquisition of additional data from the vegetation monitoring on Alcedo Volcano.

#### *Floristic inventory*

Figure 2 indicates the changes in the total number of species per monitoring trip in the fourteen quadrats of 900 m<sup>2</sup>, related to the precipitation at the Darwin Station. During the first monitoring, undertaken in November 1995 (garúa season), 32 species were recorded; the rainfall was minimal. In the second monitoring survey in May 1996 (rainy season), annual species appeared, giving a total of 57 species recorded. During the third monitoring, undertaken in a new period of garúa, the number of species dropped to 50, possibly because it had stopped raining. In June 1997, there was heavy rainfall, which diminished in the months of September and November. Nevertheless, the number

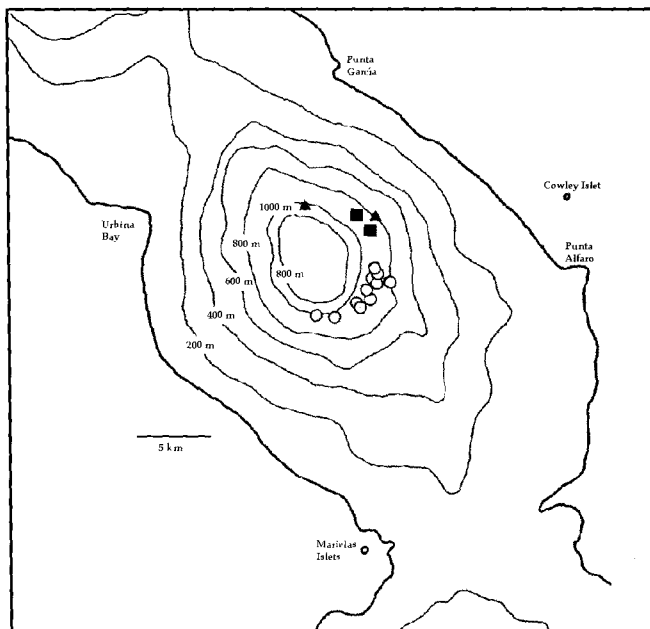


Figure 1. Map of Alcedo Volcano, Isabela Island, showing vegetation monitoring quadrats. Circles indicate the areas of the 14 permanent quadrats for vegetation monitoring; squares indicate the quadrats for the study of *Darwiniothamnus tenuifolius*; and triangles indicate the quadrats for the study of *Scalesia microcephala*.

of species recorded remained high in November. The highest peak in rainfall was in April 1998, when the greatest number of species, 102, was recorded. Six months later, this declined to 86 species, probably due to the dry season then prevailing in the islands.

In other sites, uncommon species were found, such as *Phytolacca octandra* (native), *Jaltomata werfii* (native), and *Pleuropetalum darwinii* (endemic).

*Variations in the native vegetation due to rainfall*

The majority of plants on Alcedo are abundant during the rainy season. A case in point is *Ipomoea alba*, which was not found in any of the regular monitoring quadrats until June 1997, but, during the winter and with the appearance of El Niño, it recovered remarkably, forming very dense patches. In the last monitoring, carried out in October 1998, the vegetation in general had suffered serious modifications, particularly *I. alba*, due to the drought and the continuing destructive action of the goats. In addition, the percentage cover of *Paspalum conjugatum* increased enormously during the rainy season, probably because it is a grass resistant to competition from other herbs.

In general terms, the vegetative cover was high during the 1997-98 El Niño. Apart from *I. alba*, the dominant and common species that covered the soil in the humid zone (south) of the volcano during El Niño were the following: *Borreria laevis*, *Cyperus brevifolius*, *Dichondra repens*, *Pteridium aquilinum*, *Cuphea carthagenensis*, *Plantago major*, *Hyptis rhomboidea*, *Physalis pubescens*, *Elaterium carthagenense*, and *Sida rhombifolia*. Figure 3 shows the variability in vegetative cover and includes the species that are considered most frequent

and, at the same time, the most abundant, during the monitoring on Alcedo.

*Appearance and dispersion of introduced species*

El Niño may have favored the appearance of some introduced species, such as *Ricinus communis*. About ten adult plants of 3 m height were found, along with a good number of subadults and seedlings. The plant had previously been recorded at the site and it is likely that dormant seed had remained in the soil until helped to germinate by Niño rainfall. The area of dispersion of this introduced plant was just on the slopes of the southeastern side of the volcano (200 m north of vegetation monitoring quadrat No. 12). The individuals of this species were eliminated immediately and the seeds collected and burned. Other introduced species that appeared, in order of dominance, are *Sida rhombifolia*, *Hyptis rhomboidea*, *Plantago major*, *Synedrella nodiflora*, *Eleusine indica*, *Cuphea carthagenensis*, *Sonchus oleraceus*, *Stachytarpheta cayennensis*, *Canna lutea*, and *Datura stramonium*. The most aggressive species, given their dispersal and invasion of large areas, their displacement of native herb species, and the possible impediment to the natural regeneration of *Scalesia microcephala*, *Darwiniothamnus tenuifolius*, *Tournefortia rufo-sericea*, *Zanthoxylum fagara*, and *Cordia leucophlyctis*, are for the most part *S. rhombifolia* and, to a lesser extent, *H. rhomboidea*.

*Growth in diameter of marked trees and bushes*

The measurement of diameter at breast height (DBH) of trees and bushes within the vegetation monitoring quadrats began in May 1996, with the marking of 438 individuals of the following species: *Scalesia micro-*

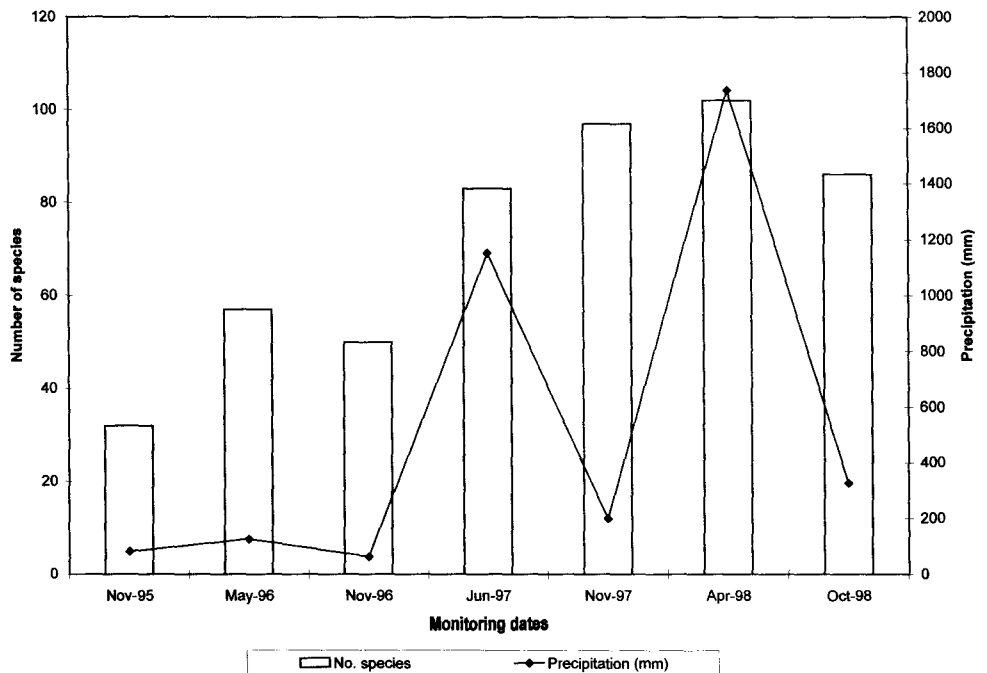


Figure 2. Changes in the total number of plant species in relation to climatic changes during monitoring of quadrats on Alcedo Volcano. Data on precipitation provided by the meteorological station, CDRS. Accumulated precipitation during each period of the study.



DISCUSSION

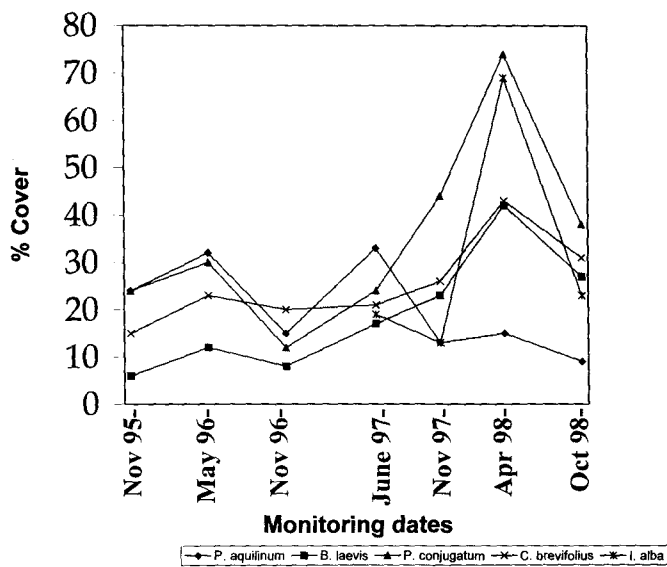


Figure 3. Variations in cover by predominant species during the vegetation monitoring on Alcedo.

*cephala*, *Tournefortia rufo-sericea*, *Zanthoxylum fagara*, *Croton scouleri*, *Psidium galapageium*, *Cordia leucophlyctis*, and *Ichroma ellipticum*. The largest diameters were those of *Zanthoxylum*, *Scalesia*, and *Tournefortia*, which varied between 20 and 25 cm. The growth of DBH during the first year, May 1996 to June 1997, is slightly less than that which occurred in the second year, June 1997 to October 1998 (Figure 4).

Mortality of marked trees and bushes

During the first year of the monitoring project, the greatest decrease in the number of individuals was in *P. galapageium*, *C. leucophlyctis*, *T. rufo-sericea*, and *S. microcephala*. During the second year, there was a greater percentage of trees and bushes that died, with the species affected being the same as during the first year, as well as *C. scouleri* on this occasion (Figure 5). Evidently, the high rainfall, combined with the steep slopes, caused many of the trees to fall and consequently die. The population of *Darwiniothamnus tenuifolius* suffered a great decrease; in 1996 about 150 plants of this species were recorded in the quadrats established for its study, while in 1997 only 21 were found, and in 1998 the number dropped to 12. Possible causes of death of the plants were the excessive rainfall, consumption by goats, and the invasion of *S. rhombifolia*, an introduced plant that currently seems to be impeding the regeneration of *Darwiniothamnus*. The regeneration of tree and bush species in the humid forest zone increased after winter and El Niño, particularly *T. rufo-sericea*, *S. microcephala*, *C. scouleri*, *Solanum erianthum*, and *Psychotria rufipes*.

According to the monitoring that has been conducted to date on Alcedo Volcano, we can state that the number of plant species varies markedly in relation to the intensity of rainfall, with the number of species being greater during El Niño. According to the reference rainfall data, the rainfall decreased progressively from June until November 1997, with light rains, which allowed the number of species to continue increasing. However, from April to October 1998, there was an abrupt change in the weather; heavy rains lasted until May, after which there was a period of drought. This is the most probable reason that fewer species were found in the monitoring of October 1998. On the other hand, it is possible that this variation is related to the campaigns to eradicate introduced mammals. Hamann (1985) and Luong (1985) indicate that there was an increase in species, particularly herbaceous ones, during El Niño, followed by a decline in the number of species during the subsequent "La Niña" drought. This pattern seems to be occurring the current El Niño-La Niña cycle on Alcedo.

One of the species on Alcedo whose increase depended on the rainy or very rainy season is *I. alba*. Van der Werff (1978, 1985) and Hamann (1981) indicate the presence of this species, forming a dense mat over trees and bushes. During the 1982-83 El Niño, this climbing species covered extensive areas in the south-east, east, and northeast inside and outside the crater of Alcedo, forming impenetrable thickets of vegetation (C. Márquez, pers. comm.). Subsequently, the population of *I. alba* decreased due to the lack of rainfall and, above all, consumption by goats (Freire 1992). In April 1998, this climbing plant was dominant and we observed extensive patches on the rim of the volcano, the upper slopes, and the lower slopes, but in October of the same year, it was uncommon to find these dense patches.

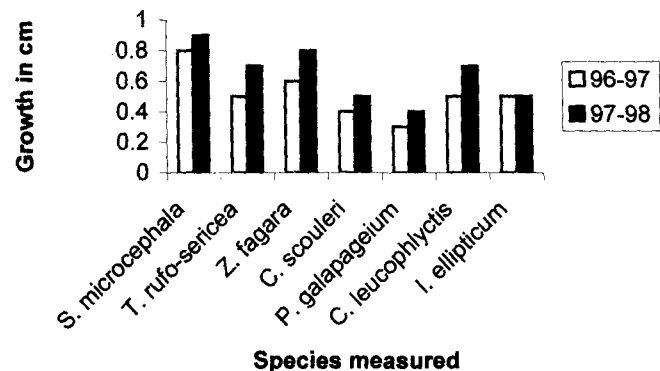


Figure 4. Average annual growth of DBH of marked trees and bushes alive until October 1998.

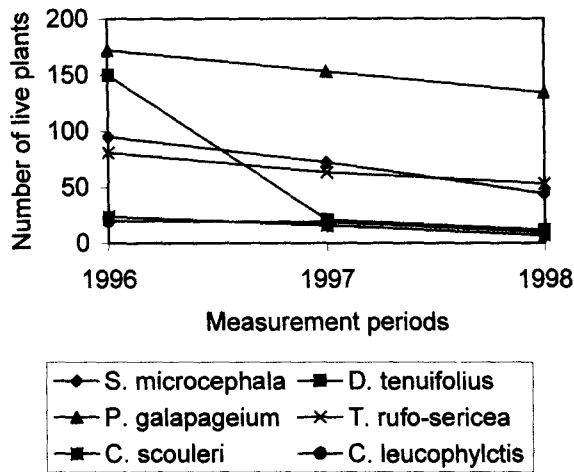


Figure 5. Annual decrease in the number of plants for the measurement of DBH and *Darwiniothamnus tenuifolius*, until October 1998.

Nevertheless, it may recuperate with the next rains. On the other hand, figure 3 shows the decrease in the percentage cover of *P. aquilinum*, perhaps due to the competition that occurred just when *I. alba* was recorded for the first time, in the monitoring of June 1997. *I. alba* totally covered *P. aquilinum*, impeding its regeneration and survival. In the last months of 1998, it was observed that the soil had been eroded by the rains and the presence of introduced mammals, which has given rise to areas devoid of vegetation.

*Ricinus communis* is considered invasive in the Galápagos Archipelago. It disperses rapidly in the rainy season. Van der Werff found some plants on Alcedo in 1978; subsequently they were eliminated by the Galápagos National Park Service, but possibly some seeds remained that germinated in 1998. Once again this species has been eliminated and the seeds burned. Nevertheless it is advisable to frequently visit the area where this plant was most recently found. Other introduced species that have expanded rapidly throughout Alcedo are *S. rhombifolia* and *H. rhomboidea*. These species were recorded by van der Werff (1978), Hamann (1981), Lawesson (1987), and Freire (1992). According to the vegetation monitoring, *S. rhombifolia* was first found in May 1996, while *H. rhomboidea* was found in June 1997. During the last monitoring, in October 1998, we observed that *S. rhombifolia* had become a potentially damaging species, with individuals up to 2.5 m high. Apparently this species decreases during periods of drought, but it has a great number of seeds that remain dormant in the soil, awaiting a period of rain to reappear with vigor.

The forest benefitted from the quantity of rainfall and showed an excellent natural regeneration of bushy and tree species during El Niño. The opposite occurred with adult trees and bushes that grow on the fragile soil and the middle slope of the volcano. These were at greater risk of dying due to the erosion caused by the formation of rivulets and gullies. With respect to the slight increase in

DBH in trees and bushes alive during 1998, it seems that there exists a direct influence from the rains; this should become clearer following further monitoring periods.

## ACKNOWLEDGMENTS

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## EFFECTS OF THE 1998 EL NIÑO ON DARWIN'S FINCHES ON DAPHNE

Peter R. Grant and B. Rosemary Grant

El Niño events are amplifications of normal seasonal processes in the eastern tropical Pacific region (Philander 1990), and they bring an abundance of rain to the Galápagos. Since 1973 we have been studying how populations of Darwin's finches on the small island of Daphne Major respond to conditions that vary from droughts of scarcity to El Niño years of plenty. For us this variation is like a gigantic watering experiment that decreases or increases the food supply of the finches (seeds, caterpillars, spiders, pollen, nectar, etc.) at the normal time of breeding, while leaving other potentially influential factors either unaffected (photoperiod) or affected in a minor way (temperature). The experiment is not under our control, nevertheless we can learn a lot by comparing the responses of finches in different years. The finches in question are four species of *Geospiza* ground finches: large (*G. magnirostris*), medium (*G. fortis*), and small (*G. fuliginosa*) ground finches, and the cactus finch (*G. scandens*).

We have studied finches on the island throughout the entire breeding season in four El Niño years (1982-83, 1987, 1991, and 1998), as well as ten other years of breeding (Grant *et al.*, ms.) and three other years of drought and no breeding (1985, 1988, 1989). Three features of breeding vary among years. They are the number of eggs a female lays in a clutch, the success in raising the young to the point of fledging, and the number of times a female breeds. The sum total of these components is the annual production. Production is on average four times higher in El Niño years than in non-El Niño years. The main reason for the high production is that finches breed four to eight times in El Niño years, instead of the usual one (or none) to four times in non-El Niño years. Clutch sizes are also larger in El Niño years than in non-El Niño years, and fledging success is slightly higher in El Niño years, although hatching success tends to be a little lower in part because the foraging of the parents is interrupted by rain. Remarkably, in the longest breeding seasons of all (1982-83 and 1987), young finches hatched at the beginning of the season were breeding three months later and contributing to the total production; some finches became grandparents within one season!

How did the responses of finches in 1998 compare with responses in other El Niño years? Rainfall on Daphne in 1998 amounted to two-thirds of the quantity that fell in the mega-El Niño of 1982-83. This should have resulted in prolonged and prolific breeding of the finches to an extent exceeded only in 1982-83, but it didn't. A few birds bred in January following the heavy and

repeated rains that began in the last few days of 1997. By February breeding was in full swing and continued in March, April, and May, but by the second week of June, breeding had ceased. Thus the start to the breeding season was sluggish, and the end was precipitous, and neither was expected from the pattern of rainfall. For example, rain continued into early June, but finches did not continue to breed. This pattern was seen in all four species.

In two respects finch breeding in 1998 was typical of breeding in a Niño year. First, clutch sizes were distinctly higher than in non-El Niño years; clutches of five eggs were moderately common in 1998, whereas they are exceedingly rare, if they occur at all, in non-El Niño years. The larger number of eggs in a clutch suggests that females find it easier to get enough food to make eggs in Niño years, and 1998 was no exception to the rule. Second, hatching and fledging success were also about the same as in other El Niño years. The anomalously low production in 1998 was clearly brought about by an unexpectedly short breeding season. Why?

More specifically, why did breeding start slowly and end rapidly? Normally, the length of the breeding season appears to be governed by a food supply that is replenished for as long as the rain continues. In 1998, the length of the breeding season was not so clearly determined by the pattern of rainfall, but perhaps the populations of caterpillars took a long time to increase, and then decreased quickly at the end of May. Our previous work on both Daphne and Genovesa (Gibbs and Grant 1987, Grant and Grant 1989) makes this a plausible explanation. However, at best it is only partly correct; although their numbers were declining, caterpillars were still fairly plentiful in our samples in June, when finch breeding had all but ceased.

The explanation may lie instead in a combination of unusual conditions; high initial densities of finches and exceptionally high temperatures. Breeding may have been delayed as a result of much interference. An unknown factor that might have contributed to the delay is a carry-over effect from the extensive breeding in the previous (El Niño) year; finches may not have been physiologically ready to breed when the rains returned at the end of 1997. Breeding ceased early in 1998, perhaps because the energetic benefits gained from a declining food supply was offset by rising energetic costs of nest and territory defense as overall density, adults and fledglings combined, increased. High air temperatures may have contributed to the increase in

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 DISPERSAL 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 Galapagos 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 lecheguana* 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.

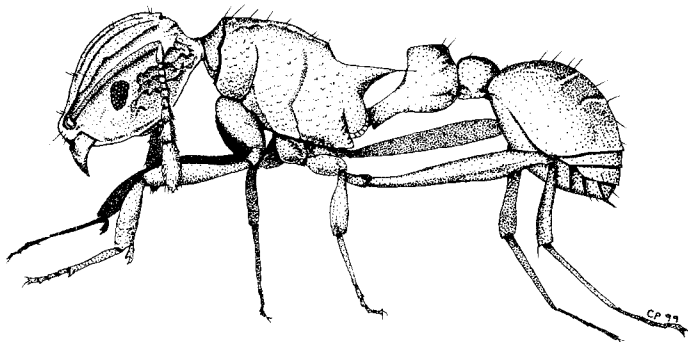
In this article, we present a summary of observations of the behavior of these species during the El Niño event of 1997-98, including new distribution records.

### 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 (Silberglie 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.

Figure 1. *Wasmannia auropunctata*.  
Drawing by Christine Parent.



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

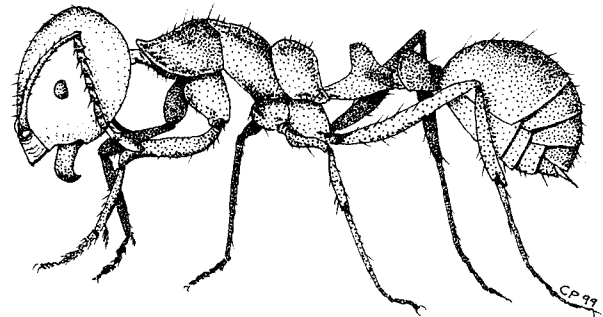
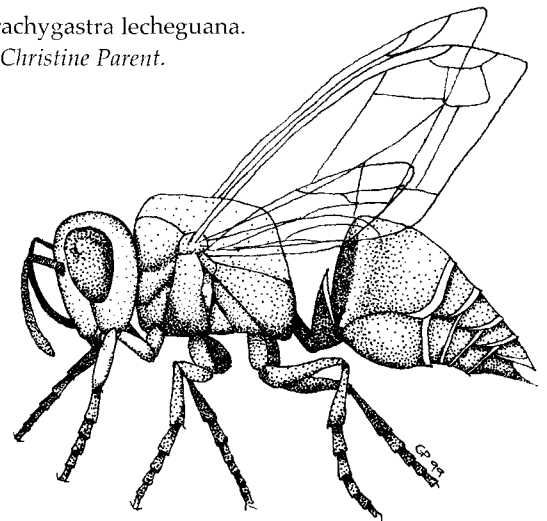


Figure 2. *Solenopsis geminata*. Drawing by Christine Parent.

Figure 3. *Brachygastra lecheguana*.  
Drawing by Christine Parent.



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

(Roque 1998). 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

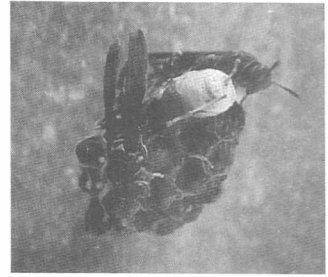
*Solenopsis geminata* (Fabricius), the tropical fire ant (Figure 2), was also introduced at the turn of the century (Wheeler 1919) and has now colonized the islands of Santa Cruz, Floreana, Isabela, and San Cristóbal. *S. geminata* is a voracious feeder on invertebrates and may have an impact on the 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

Figure 4. *Polistes versicolor*  
Photograph by  
Lázaro Roque-Albelo.



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*.

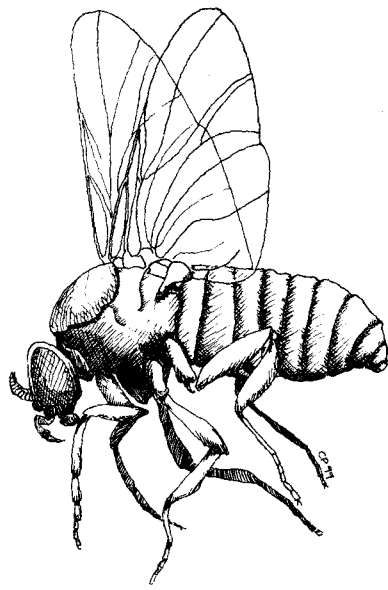
During the months of heavy rainfall from December 1997 to May 1998, population numbers of both these species diminished. Low numbers were recorded at the commencement of a monitoring program in June 1998, with numbers increasing once the dry season set in. Large numbers of *Polistes versicolor* are observed 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

Figure 5. *Simulium bipunctatum*.  
Drawing by  
Christine Parent.



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.

## 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 galapagosa*. 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 seychellarum*, 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 (e.g., Santa Cruz, Santiago, and Isabela). 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



Figure 6. *Icerya purchasi*. Photograph by Lázaro Roque-Albelo.

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 (Beardsley 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.

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

tine system. 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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