

# NOTICIAS de Galápagos

No. 55 July 1995

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While emphasizing that the continuing success of conservation in the Galápagos is directly dependent on the receipt of future contributions, we wish once again to state our deep gratitude to all those supporters whose generosity has made it possible to achieve so much since the establishment of the Charles Darwin Research Station and the Servicio Parque Nacional Galápagos.

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**We are grateful for your steadfast support and help.**





## NOTICIAS DE GALAPAGOS

A Publication about Science and Conservation in Galápagos,  
the Galápagos National Park Service, and the Charles Darwin Research Station

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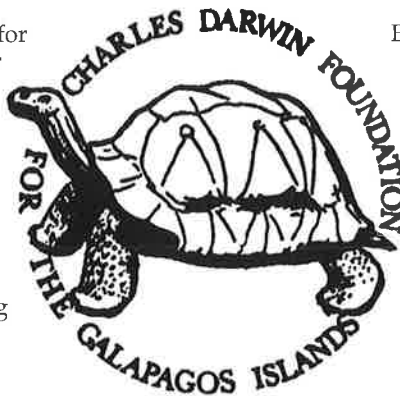
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## A BRIEF ACCOUNT OF SOME EARLY INHABITANTS OF SANTA CRUZ ISLAND

By: J. P. Lundh

In 1953 the Norwegian Archaeological Expedition, led by Thor Heyerdahl, found pre-Columbian potsherds on the northwest shore of Santa Cruz (Whale Bay). In the following year, the Walt Disney Expedition found similar remains at Cerro Colorado, on the northeast side of the island. These shards have been identified as originating from the coast of Ecuador and northwest Perú. Their Indian makers possibly visited Galápagos for limited duration as there is no evidence of colonization from this time. I originally agreed with many people who thought that the shards may have been carried to Galápagos by later visitors after the Spanish discovery of the archipelago. However, my opinion has changed after carefully reading a paper published by Heyerdahl and Skjølsvold (1956). The material seems too abundant and comes from several types of pottery spanning several cultural periods. My conclusion after going through the paper is that indigenous people from the mainland probably visited the islands over a considerable period, until the Inca conquest of north west Perú. While it is true that some of the more recent pottery belongs to styles that overlap the Inca presence in northwest Perú, no Inca pottery shards have been found in Galápagos. If indigenous pottery was brought over in colonial times, Inca pottery should have been present. I do not believe, as do Heyerdahl and Skjølsvold, that pre-Columbian fishing activities in Galápagos survived into colonial and post-colonial times. They most likely died out with the fall of the Chimú kingdom in Perú.

Humans probably first inhabited Santa Cruz during the time of General Villamil in the 1830's. At this time there were two or three shacks at the foot of the hill in Whale Bay. In 1846, Henri Louns (Compte de Gueydon), commanding the French vessel *Le Genie*, visited this site from February 7 - 11. He writes of people living near the shore and mentions a trail leading inland to a spring. The spring is most likely the one at Santa Rosa. He makes no mention of the occupation of the inhabitants. However, it is likely that they were engaged in hunting tortoises for Generals Villamil and Mena.

General Villamil had a long history in Galápagos. He resigned as governor and left the islands but came back several times and had General Mena there to look after his interests. In fact, in 1852 he gave Captain (later Rear Admiral) Christian Adolf Virgin written permission to supply himself with cattle on Floreana, for the crew of His Swedish Majesty's Frigate "Eugenie". Villamil was twice governor of Galápagos and he returned with a six-month leave (he was then Commandant General of the Guayas

District) in 1847. In 1854 he sailed out with an expedition that was to confirm whether guano really existed on the islands. He was bitterly disappointed.

General Mena's record in Galápagos is harder to trace. I have not even found the gentleman's first name. There is very little on record about him, though his name keeps appearing everywhere in the 1840's and 1850's when the Galápagos are mentioned. He most likely had distinguished himself in the War of Independence and may have served together with General Villamil — they certainly were good friends.

In May 1852 Nils Johan Andersson, traveling on board the Swedish frigate *Eugenie*, collected the first botanical specimens from Santa Cruz at Whale Bay. He found two dilapidated shacks at the foot of the hill above the beach. When he and his companions approached shore they saw a few men fleeing inland. Upon landing they discovered a woman in one of the dwellings, but could not communicate with her, as none of them knew Spanish.

According to San Cristóbal tradition the orchards and crop plantations found at Santa Rosa and Salazaca, inland from Whale Bay, were planted upon orders from don Manuel J. Cobos in the late 1800s, in order to provide food for his tortoise hunters when they worked in the area. Whale Bay was then known to the settlers of San Cristóbal as "Puerto de las Chacras" — Harbor of the Farms, and the hills inland were called "Sierra de las Chacras".

In the 1940's oranges, limes, cassava, taro, sugar cane, plantains and bananas were still to be found at Santa Rosa. Donkeys brought to the island by the tortoise hunters had not yet spread from the lowlands, and pigs and goats, introduced in the late 1920's to the south side of the island, still remained near their area of introduction.

Around 1910 the first long-term settler established himself near what is now called Bellavista. This was an old Mexican called Felipe Lastre, one of Sr. Cobos' previous foremen. Some time later, an American and an Englishman came to live on the island. In 1925, five men arrived at Bellavista from San Cristóbal. They brought with them a few head of cattle purchased by a Guayaquil businessman who hoped to begin a cattle ranch on Santa Cruz. One of the men optimistically named the place where they settled "Hacienda Fortuna".

In 1926, shortly after the first Norwegians founded Puerto Ayora, the men at Hacienda Fortuna (Bellavista) returned to San Cristóbal. Lastre also left about that time. Elías Sánchez was the only original settler to remain, tending a small farm beside the trail to Hacienda Fortuna until 1938.

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## ELECTRONIC MAIL COMES TO GALÁPAGOS

By: Jim Pinson

*[Electronic mail (e-mail) is a mailing system that works through telephone lines connecting a network of computers (the Internet, a.k.a. the Information Super Highway). It allows mail to be sent around the world to anyone with a computer connected to the network. It is much faster than postal mail and often instantaneous. E-mail conversations can be carried back and forth almost as quickly as if talking over the phone. However, unlike the telephone, service costs for long-distance e-mail service are subsidized by participating governments. E-mail messages are stored so that the recipient need not be sitting at his or her computer when the originator sends the message. This storage system also prevents loss of messages in the event of a power outage or breakdown of a computer. - Editorial Staff]*

Two years ago, electronic mail (E-mail) seemed like only a dream for the Charles Darwin Research Station (CDRS). The station's existing communication system desperately needed improving. The phones seldom worked, and long distance service was unreliable and expensive. Postal mail was slow and also unreliable. Use of satellite dishes was prohibitively expensive. A fast, reliable and affordable means of communicating with the rest of the world seemed out of reach. Those of us who were accustomed to using E-mail dreamed of having it in Galápagos.

Prospects for getting E-mail improved one day in October 1992, with an unexpected visit to the station by Xavier Baquero, from the Banco del Pacifico (BP), Ecuador, and Steve Goldstein of the National Science Foundation (NSF) of the United States of America. As a service to the community, the Banco del Pacifico was offering free Internet access to nonprofit organizations. The staff at CDRS needed little convincing and readily accepted the generous offer.

E-mail did not become a reality at CDRS until May, 1993. Although the Banco del Pacifico in Puerto Ayora would provide access to the Internet, the station had to find a means of connecting with the bank about 1 km

away. The most obvious method was to dedicate a phone line for the purpose, but that would be expensive and unreliable.

David Anderson, a long time proponent of E-mail at CDRS, searched for both the appropriate technology and the necessary funds. He found that NSF could fund the equipment, but only if it was added as a special request to a pre-existing NSF grant. Howard Snell came to the rescue by offering to buy two radio modems on his NSF grant. These modems would provide fast and reliable communication to the bank. Dave Anderson hand carried the modems and antennas to the station on his next research trip. The modems were soon installed, and the antennas aligned by two communications specialists from BP. At long last the station was on-line!

After a few months, it became obvious that the original system of software wasn't filling the needs of the station. Because I had experience in computer programming for networks, I was drafted to design a new system. Galápagos Mail, or G-Mail is the result. It is a fusion of the original system with two free software packages. The Pegasus mailer was linked to the Ham radio package KA9Q using special software developed at the station.

G-mail has the special ability of allowing messages to be created and read on a floppy diskette. The diskette must then be taken to the computer center at the station in order to actually send and receive the messages. Mail stored on the diskette can then be read and new messages can be composed on a computer outside the station if need be. This system is especially useful for visiting scientists. Mail messages can be written on a personal laptop computer in the field, then copied onto a diskette which can be sent by boat to the station, from where they can be mailed. Conversely, incoming mail can be copied onto a diskette and returned to the scientists in the field where it can be read on their personal computer.

E-mail quickly became a part of every day life at the station. Scientists used E-mail to arrange trips with the

staff, communicate with field camps and send data overseas. Staff members at the station were able to consult with colleagues around the world. The importance of and dependence on E-mail at the station became obvious when the modem failed and the station was without E-mail contact for over a month. It was quite a relief when a spare modem was brought to the station to prevent E-mail from vanishing again. As with so many things, you don't appreciate something until it is gone.

The E-mail system at the station continues to evolve. A UNIX server, designed to handle mail more reliably, has just been installed. A more extensive network is currently being installed, providing Internet access to several more computers at the station. Soon the staff will be

introduced to the "World Wide Web" (WWW), an information network offering access to libraries, scientific data sets, and news on the latest developments in science from around the world. Not only can this service be used from CDRS to obtain information from around the world but CDRS plans to eventually become a WWW site itself, contributing information about the station, personnel, research projects, and even select data sets. The next time you venture on the "Information Super Highway", keep your eyes open for a giant tortoise, moving slowly but surely forward.

**Jim Pinson, Charles Darwin Research Station, Isla Santa Cruz, Galápagos, Ecuador.**

## FUNDAMENTALS

**By: Godfrey Merlen**

The eruption on Fernandina Island that occurred toward the end of January 1995 was a spectacular event. For the first time in many years, a large number of people were able to witness a geological "hot spot" in action. The copious quantities of lava that reached the ocean to the west and the interconnecting rivers of fast-flowing molten rock left all who saw it with a powerful image of light and energy. At night, the lurid red clouds painted against the dark sky gave the impression of a penetrating ball of light. Perhaps even Benjamin Morrell would have been impressed by this awesome sight. Unfortunately, pitch is not a chandler's item these days and it was not possible to repeat his observations of 1825!

I visited the area on three separate occasions (January 27-30, February 6-7 and March 18-19). I was authorized to land with André Mauchamp on the second trip and with Mitsuaki Iwago and Kiyoshi Yokokawa from NHK (Japanese National Television) on the third trip. I plotted positions of the forming fissures, cones, and lava flows using a portable GPS (Global Positioning System) instrument because observational satellites are out of commission and no aerial photographs of this event will be forthcoming.

On the night of February 6, while near the source of the eruption, I noticed that a strong flow had developed south of the general pattern of lava channels to the west. This new flow headed with unerring accuracy toward the landing at Cape Hammond. On the morning of the 7th, I crossed a smoky lava field to Iguana Hill, part of an old cone surrounded by new lava, and climbed to its top. The hill is about 1 km from the "source". At the foot of the hill, the flow diverged and huge quantities of molten rock rushed

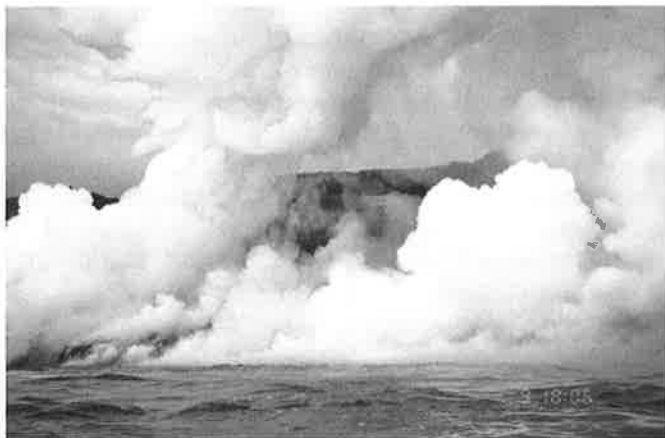
westward in fast-flowing rivers. These rivers occasionally became dammed with enormous, semi-solid boulders the size of houses. On breaking free, the magma surged down steep lava falls with the fluidity of water. Vegetation vanished in spurts of flame and puffs of smoke.

The huge red flows were a striking contrast to the silver-grey palo santo trees on top of the hill, many of which had been felled every-which-way by the initial release of pressure from the eruption. Behind me, the center of the growing source cone displayed a continuous fountain of molten material, falling as scoria hundreds of meters away. By day, the fountain was blood red; by night, a golden arc.

Upon descent, I found that the lava flow had cut off my easy retreat across a large pahoehoe field. Its length was about 4 km, leaving over 1 km between its front and the landing at Cabo Hammond. This front has not advanced, but that day I could see the white-hot interior through cracks between boulders, indicating some movement was still occurring. Several smaller flows have since moved in the same direction between February 6 and March 6, but no more than about 1.5 km from the cone.

Cape Hammond offers a refuge from the swells that continuously batter the coastline from the south. It is the only protected landing between Cape Douglas in the north and Punta Mangle to the east, since wave action has produced vertical cliff faces on the west and south sides of the island. The small bay at the landing is thus a unique feature of this coast and is the result of previous lava flows to the south; an accident of time and place. The bay, with its two boulder beaches and a sandy beach behind a shallow protected pool, is a haven for endemic fur seals, flightless cormorants, marine iguanas, and penguins. Even





Photographs of the Fernandina eruption taken in March 1995 by Susan Noftsker.

though the eruption is a totally natural event, there is human concern for this unique, remote spot behind which the gaping earth is transforming the face of the land irrevocably and irreparably. The same forces that created the Galápagos are now facing the life forms molded by natural selection on these islands. Nonetheless, in these animals I saw no fear of what might be, no collapse into panic or immobility in the face of imminent disaster – reactions which might well have been our own. The fur seal pups leaped and played in their secure pool. The cormorants dried their wings on the small point between the boulder beaches. They were even attempting to breed – one pair now has two eggs in a well-made alga nest. While a smoke pall drifted over the bay, marine iguanas were digging nests in the dark sand beach behind the fur seal pool. Even when the sea temperature in the bay rose to 32°C and the surface turned green, the animals proceeded as if nothing had happened. Life is naïve; perhaps that is why it has survived in spite of the physical dynamics of an often volcanic planet.

On the other hand, thousands of fish died when copious amounts of lava plunged into the water, violently changing the natural rhythm of the sea. Low-frequency, echoing explosions could be heard through hydrophones, miles offshore. The temperature near the coast rose to boiling point. Violent upwellings of cold water, which seemed to be the result of molten lava entering the sea, were juxtaposed with this steaming cauldron. Stresses of pressure, temperature, acoustics, and chemistry exceeded the limits that fish could tolerate. The seabirds took advantage of the mass piscine mortality. Eels, damselfish, scorpionfish, and serranids were eagerly devoured by frigatebirds and pelicans. Some birds were scalded in the process of diving for food. A number of marine iguanas, following their life course too close to the lava flows, were doomed. The coastal alga beds were destroyed. Some iguanas, in the path of the molten lava, reacted to the increasing heat by raising their bodies in their ancient way of cooling themselves. As the heat increased, they tried moving to higher ground, which in some cases meant

walking directly onto flowing lava, where the extreme temperatures overwhelmed them.

High up on the flank of the volcano, where the lava pumped forth onto the surface of the island, land iguanas also perished in the confusion. One land iguana had moved onto a new lava slope which was still blisteringly hot when I arrived. The dead animal stood immersed in the lava, with its head strained upward, its tail tightly coiled, and arms stretched to full extent – its extremities had vanished. Cactus plants surrounding the cone were blistered on the side facing the heat; many other species of shrubs appeared dead. The palo santos stood with golden brown leaves, crisped by the earthly furnace.

On my second visit to this highland region (March 18-19), I was able to approach, through the smoke, to the base of the cone. There I found land iguanas crunching over the deep scoria bed and saw, under the black slopes of this new slag heap, an iguana raise itself up while a mockingbird removed parasites from its red-gold legs. I saw the land iguanas tucking in on the new, fresh leaves that were pushing forth from the shrubs that I had previously thought dead. Within a meter of the still hot lava, an *Opuntia* cactus had put forth new pads and flowers. Amidst the tangle of broken palo santo trees torn from the ground, the silver bark split from the brown-gold sapwood beneath, the new volcano in its awesome and beautiful fury showered down scoria, which in a little while will produce new soil. Life on this planet is naïve, but has an opportunism built into it that is capable of dealing with such bizarre situations.

If all that we see happening in this absolutely natural event is acceptable, why should we be concerned for the life at the Cape Hammond landing? In part, it is because of what we have learned of the fragility and vulnerability of Galápagos life. The physical forces that affect the solid part of the planet are unpredictable. Their expression is primitive and awesome and their effects are uncontrollable. The life on these oceanic islands is naïve and helpless when faced with extremes. Perhaps the tortoise population on Fernandina was annihilated by eruptions such as

this one. The same week that I ventured on land at Cape Hammond, I also went ashore at Punta Mangle, a mangrove haven on the southeast corner of Fernandina. Tied to the island was a dinghy with eleven loose goats on it. I rubbed the head of one and she seemed to appreciate it in her innocence. If given a chance, these goats, innocent of impending doom, would at a moment's notice step onto the molten lava flows in order to reach the vegetation.

After the volcano has silenced itself, perhaps black rats will arrive. Perhaps cats. In these days of change,

[Editor's Comment: In Noticias 54 the article "Visitors from the West" by Godfrey Merlen incorrectly remarked on the absence of records of the red-shouldered (also known as the red-spot or blue-lined) wrasse (*Stethojulis bandanensis*) from the eastern Pacific. This wrasse, however, has been previously recorded from Cocos Island in the eastern Pacific (Lopez, M.I. and Bussing, W.A. 1982. *Rev. Biol. Trop.* 30: 5-26; Bussing, W.A. 1985. *Rev. Biol. Trop.* 33: 81-98). In addition, recent investigations at Clipperton Atoll reveal an abundant population of this species. *S. bandanensis* is also listed in "Fishes of

the sapphire-eyed cormorant and the myopic penguin are in their last haven, for all other areas where they live are irreversibly altered. Any loss of their populations seems to jar at our well-being. In their naïveté, they will vanish forever, without regret. Only we fear the future, unable to control the volcanoes of our own minds, which threaten us and confound our capability to defend a dying world.

**Godfrey Merlen, Charles Darwin Research Station, Isla Santa Cruz, Galápagos, Ecuador.**

*the Tropical Eastern Pacific" by Gerald R. Allen and D. Ross Robertson (Crawford House Press, Bathurst, Australia 1994) as "widespread in the tropical Pacific Ocean from Australia to southern Japan, and eastward to islands of the eastern Pacific, including Isla del Coco, Clipperton Island and the Galápagos, usually associated with coral reefs". Thus far their occurrence in the tropical eastern Pacific is limited to offshore islands. We thank Godfrey Merlen, Jerry Wellington and Gayle Davis-Merlen for providing this correction.]*

## RE-IDENTIFICATION OF THREE DOLPHIN SKULLS IN THE MUSEUM OF THE CHARLES DARWIN RESEARCH STATION

By: Daniel M. Palacios

While working for the Whale Conservation Institute in Galápagos between February 1993 and March 1994, I undertook a study documenting the remains of cetaceans that have been found washed ashore on the islands. Some preliminary results are presented here, including the re-identification of three specimens from the reference collection of the Charles Darwin Research Station.

Of the 22+ cetacean species that have been observed in Galápagos waters (Day 1994), 13 are represented by beached specimens collected since William Beebe's expedition in 1923 (Palacios 1995a) (Table 1). The remains of a rough-toothed dolphin (*Steno bredanensis*) (Orr 1965), and a ginkgo-toothed beaked whale (*Mesoplodon ginkgodens*) found on Genovesa in 1970 by Tjitte de Vries (Palacios 1995b) provide the only evidence that these two species occur in Galápagos. *S. bredanensis* prefers warmer waters than those normally found around Galápagos and *M. ginkgodens* has never been seen alive anywhere.

At least 29 specimens are housed in 8 scientific collec-

tions and 19 more are housed in private collections (Palacios 1995a). The museum of the Charles Darwin Research Station alone contains a reference collection of at least 22 specimens representing six species (Table 1).

I examined several of the specimens at the Charles Darwin Research Station and found that three skulls (catalogue numbers V-857, V-858 and V-859) collected by J. Webb on 1 April 1975 from the northwest coast of San Cristóbal and labeled as short-beaked common dolphins (*Delphinus delphis*) did not match those typical for that species. Close examination of the ventral side of the rostrum revealed the absence of the two deep lateral grooves running longitudinally on the left and right palatine processes of the maxillaries (also known as the palatal carination) which distinguish the genus *Delphinus* from all other genera of delphinids (Tomilin 1967; Evans 1994). In addition, I counted only 35-41 teeth (or alveoli when teeth were absent) in the upper and lower jaws of these specimens, as opposed to 45-50 teeth (or alveoli) in the jaws of other *D.*

**Table 1.** List of cetaceans recorded from remains in Galápagos. Asterix indicates specimens in the reference collection of the museum of the Charles Darwin Research Station (CDRS).

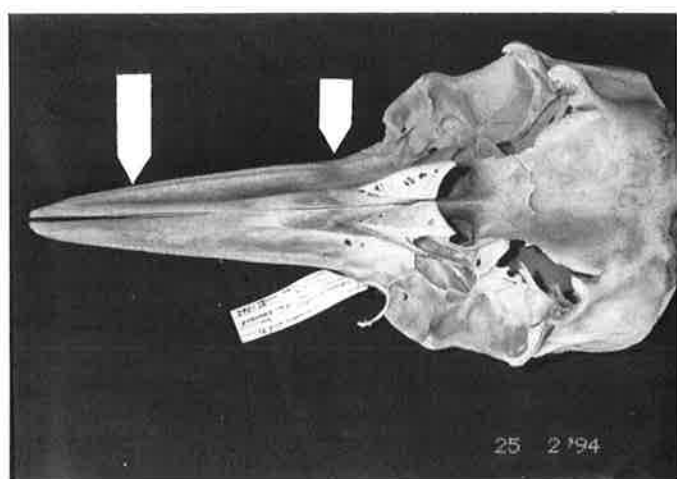
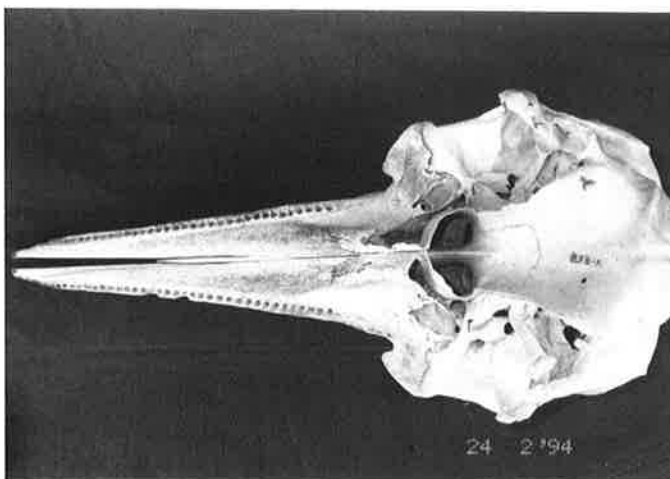
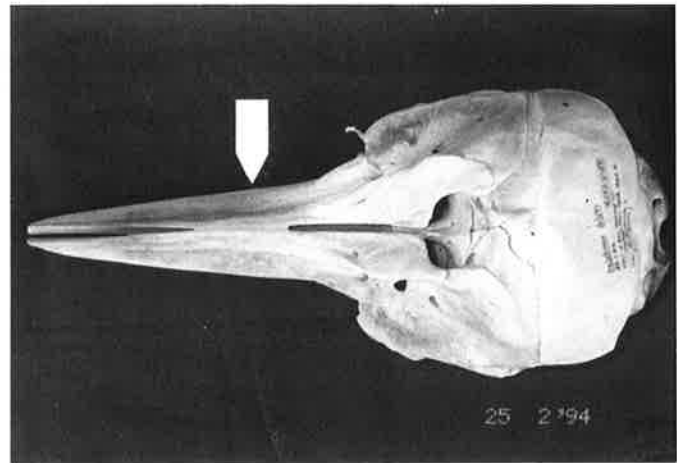
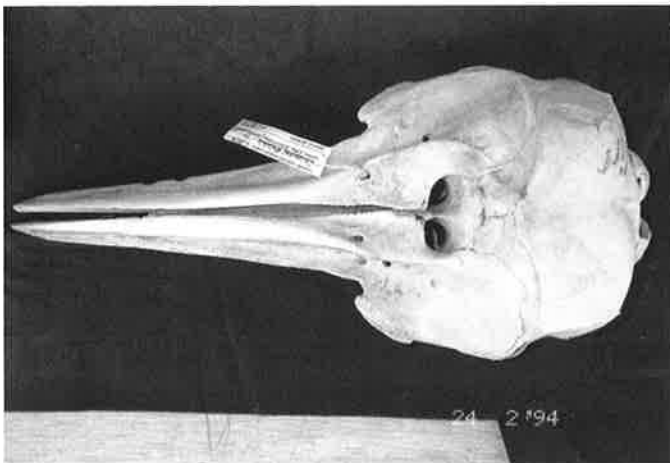
<u>COMMON NAME</u>	<u>SCIENTIFIC NAME</u>
Rough-toothed dolphin	<i>Steno bredanensis</i>
Risso's dolphin	<i>Grampus griseus</i>
Bottlenose dolphin	<i>Tursiops truncatus</i> *
Pantropical spotted dolphin	<i>Stenella attenuata</i> *
Striped dolphin	<i>Stenella coeruleoalba</i>
Short-beaked common dolphin	<i>Delphinus delphis</i> *
False killer whale	<i>Pseudorca crassidens</i>
Short-finned pilot whale	<i>Globicephala macrorhynchus</i> *
Ginkgo-toothed beaked whale	<i>Mesoplodon ginkgodens</i> *
Cuvier's beaked whale	<i>Ziphius cavirostris</i> *
Sperm whale	<i>Physeter macrocephalus</i>
Dwarf sperm whale	<i>Kogia simus</i>
Rorqual sp.	<i>Balaenoptera</i> sp.

*delphis* skulls I examined (for example, specimens V-591 and V-1182). The cranial measurements also show that the skulls are smaller than the skulls of *D. delphis* in Galápagos.

These diagnostic characteristics (Evans 1994; Perrin and Hohn 1994) allowed me to re-identify specimens V-857, V-858 and V-859 as pantropical spotted dolphins (*Stenella attenuata*), not the more abundant short-beaked common dolphins as originally labeled (Fig. 1). William F. Perrin subsequently confirmed the re-identification of these skulls.

#### ACKNOWLEDGMENTS

This study was possible thanks to the collaboration and patience of many people who kindly allowed me to inspect the specimens under their care or guided me to sources of information. I would like to single out Linda J. Cayot, David Day, Gus Angermeyer, Heidi M. Snell, Tjitte de Vries, Gayle Davis-Merlen, Liz Pillaert and espe-



**Figure 1.** Dorsal and ventral views of skulls of *Stenella attenuata* (Cat. No. V-858) on the left and *Delphinus delphis* (Cat. No. V-591) on the right, from the reference collection of the Charles Darwin Research Station. In the ventral view, note the flat palate of *S. attenuata* (bottom left) and the grooved palate of *D. delphis* (bottom right). Also note the medial fusion of the premaxillaries in the dorsal view (top right), another character used in distinguishing *Delphinus* (Tomilin, 1967).

cially the late Mao Ortuño, who inspired and encouraged me to undertake this study. William F. Perrin confirmed the re-identification of the *S. attenuata* skulls. I also thank the Galápagos National Park Service, the Charles Darwin Research Station and the Ecuadorian Navy for providing necessary permits and logistical support. TAME kindly provided reduced airfare to the islands.

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## POLLEN DIGESTION IN GALÁPAGOS LAVA LIZARDS

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### INTRODUCTION

Pollen grains contain a rich interior of nutrients, including all the essential amino acids and vitamins for growth and development (Faegri and van der Pijl 1971, Stanley and Linskens 1974). However, the outer coat (exine) is highly resistant to penetration by digestive enzymes (Heslop-Harrison 1971) and the degree to which animals are able to use pollen as a nitrogen source is highly variable. Digestion occurs when digestive enzymes degrade the exine or penetrate the interior via the germination pore (Gilbert 1972, Stanley and Linskens 1974, Simpson and Neff 1983). The proportion of empty to full grains in the faeces of animals is thus generally considered an indicator of the extent of digestion (Brice et al. 1989).

Pollen digestion has primarily been investigated in bees and other arthropods (e.g. Gilbert 1972, Smith and Mommsen 1984, Peng et al. 1986), but has also been found in some bats (Howell 1974, Law 1992), birds (Churchill and Christiansen 1970, Paton 1981, Wooler et al. 1988, Brice et al. 1989) and marsupials (Turner 1984, Richardson et al. 1986, Goldingay 1990) (see Table 1). The western pygmy possum (*Cercartetus nanus*) and the honey possum (*Tarsipes rostratus*) are able to digest up to 100% of the pollen they consume (Turner 1984, Richardson et al. 1986),

whereas the Queensland blossom bat (*Syconycteris australis*) and another nectar-feeding marsupial, the yellow-bellied glider (*Petaurus australis*) digest only about 50% (Goldingay 1990, Law 1992). While ability to digest pollen has been investigated in several bird species, only purple-crowned lorikeets (*Glossopsitta porphyrocephala*), New Holland honeyeaters (*Phylidonyris novaehollandiae*), zebra finches (*Poephila guttata*) and budgerigars (*Melopsittacus undulatus*) have been found to digest pollen and with less than 50% efficiency (Paton 1981, Wooler et al. 1988). In contrast, the sharp billed cactus finch (*Geospiza scandens*) was recently found to digest pollen of *Opuntia echios* on Daphne Island, Galápagos with over 90% efficiency (B.R. Grant 1994, pers. comm.).

The efficiency of pollen digestion has not been investigated in lizards. The benefit of including pollen in the diet would primarily be its rich nitrogen content as well as being a source of lipids and carbohydrates. Nonetheless consumption of pollen among nectar-eating geckos is generally dismissed as accidental and having little or no nutritional importance (Elvers 1978, Thorpe and Crawford 1979, Whitaker 1987, 1987a). On the other hand, Evans and Evans (1980) and Gardener (1984) suggest that pollen may be an important component of the diet of *Phelsuma* geckos in the Seychelle Islands since at least four species

consume pollen from several species of palm, and defend pollen sources from intraspecifics. Nonetheless it remains to be determined whether these geckos are able to digest pollen and to what degree it contributes to their nutritional requirements.

Any lizard species that feeds on flowers is exposed to potentially nutrient-rich quantities of pollen. In Galápagos, lava lizards of the genus *Microlophus* (= *Tropidurus*) (Frost 1992), although primarily arthropodivorous, include plant material and bird defecations in their diet. Werner (1978) recorded both flowers and leaves in the diet of *M. delanonis* on Española Island and Schluter (1984) recorded *M. pacificus* on Pinta Island eating a variety of plant material, particularly flowers and fruit. My own observations

of *M. albemarlensis* on Daphne Island in 1990, 1991 and 1994 show that a variety of plant material is consumed, including the flowers of eight plant species (Grant 1991, East 1994) (Table 2). These observations led me to question whether pollen might offer a significant source of protein when arthropods are in short supply. This prompted an investigation in which I examined lizard faeces for evidence of pollen digestion. Here I examine whether *M. albemarlensis* is able to digest pollen from two species of flowers which comprise a significant portion of their diet at certain times of the year; *Opuntia echios* and *Tribulus cistoides*. I then discuss the implications of my findings in terms of the general feeding ecology of *Microlophus* and other omnivorous lizards.

**Table 1.** Percentages of digested pollen grains for several species of vertebrates, recorded as the percentage of empty grains found in the faeces. Note that only one bird (*Geospiza scandens*), two marsupials (*Tarsipes rostratus* and *Cercartetus nanus*) and one lizard (*Microlophus albemarlensis*) are able to penetrate the exine of significant amounts (>60%) of the pollen they ingest.

<u>CITATION</u>	<u>VERTEBRATE SPECIES</u>	<u>POLLEN SPECIES</u>	<u>% DIGESTED</u>
	BIRDS		
Paton 1981	<i>Phylidonyris novaehollandiae</i>	<i>Banksia</i>	36
		<i>Amyema</i>	12
		<i>Epacris</i>	24
		<i>Astrolooma</i>	48
		<i>Grevillea</i>	17
		<i>Correa</i>	0
		Myrtaceae	47
Wooler et al 1988	<i>Phylidonyris novaehollandiae</i>	<i>Banksia</i>	45
	<i>Melopsittacus undulatus</i>	<i>Banksia</i>	38
	<i>Poephila guttata</i>	<i>Banksia</i>	41-44
	<i>Glossopsitta porphyrocephala</i>	<i>Banksia</i>	47
Brice et al 1989	<i>Calypte anna</i>	<i>Callistemon</i>	4.7
		<i>Eucalyptus</i>	6.9
		<i>Zauschmeria</i>	3.8
	<i>Calypte costae</i>	<i>Eucalyptus</i>	0
		<i>Zauschmeria</i>	0
	<i>Nymphicus hollandicus</i>	<i>Eucalyptus</i>	18.1
	<i>Trichoglossus haematodus haematodus</i>	<i>Eucalyptus</i>	4.5
	<i>Trichoglossus h. moluccanus</i>	<i>Eucalyptus</i>	6.6
		<i>Prunus</i>	12.9
Grant 1994 pers comm	<i>Geospiza scandens</i>	<i>Opuntia</i>	90-100
	BATS		
Law 1992	<i>Scyconycteris australis</i>	<i>Banksia</i>	53
		<i>Callistemon</i>	55
	MARSUPIALS		
Turner 1984	<i>Cercartetus nanus</i>	<i>Banksia</i>	64-79
	<i>Tarsipes rostratus</i>	<i>Banksia</i>	97
Richardson et al 1986	<i>Tarsipes rostratus</i>	<i>Banksia</i>	95-100
Goldingay 1990	<i>Petaurus australis</i>	<i>Banksia</i>	53
	REPTILES		
East, this article	<i>Microlophus albemarlensis</i>	<i>Opuntia echios</i>	92.4
		<i>Tribulus cistoides</i>	89.9

## METHODS

I visited Daphne Island from 10 January to 15 February, 1994. In order to determine whether the lava lizards digest *Opuntia* and *Tribulus* pollen, I collected fresh (still moist) lizard faeces from the ground and examined the contents for pollen grains. Whenever a marked lizard was seen defecating, I collected the faeces and recorded the sex, size and identification number of the lizard. In addition, I fed two *Tribulus* flowers to an adult male lizard and retrieved a faecal sample the following day. Each faeces was placed in a vial to which five to ten drops of Alexander's stain (Alexander 1969) were added until the sample was submerged. The vials were incubated at ambient temperature (23–30°C) for 24 hours, in order for the stain to penetrate the interior of the pollen grains. A sample of the contents of each vial was placed on a separate microscope slide with a disposable pipette to avoid contamination among samples, and viewed under a field light microscope at 200x magnification. I then counted numbers of full (dark purple) and completely empty (green) grains.

In order to compare proportions of empty pollen grains found in the faeces to proportions of empty pollen grains found in the flowers, I collected pollen from a single flower from 10 *Opuntia* bushes 100 m or more apart, and from 10 *Tribulus* plants 50 m or more apart. The pollen from each flower was obtained by snipping off the anthers with clean scissors and placing them in separate ependorf vi-

als. The samples were mixed with Alexander's stain and left to incubate for 24 hours. Portions of each sample were then viewed under the microscope and numbers of full and empty grains were counted. The flower samples were treated as controls.

## RESULTS

Twenty-seven faecal samples contained significant amounts of pollen. In all but one of the samples, between 80 and 100 percent of the pollen grains were completely empty (Table 3). The exception was a sample containing 64 *Tribulus* pollen grains, only 25% of which were empty. This exceptional faecal sample was produced by a severely emaciated adult female weighing only 5.2 g for her snout-vent length (svl) of 66 mm. (In comparison, the mean weight of 52 other females of equal length was  $9.0 \pm 0.9$  g). Two other adult females in seemingly good condition (svl = 64 mm and 67 mm and w = 8.9 g and 10.5 g respectively) produced faecal samples containing 90.5% and 100% empty *Opuntia* and *Tribulus* grains respectively. One adult male (svl = 83) produced a faecal sample containing 87.7% empty *Opuntia* grains. The adult male (svl = 85 mm) to which I fed two *Tribulus* flowers, produced a faecal sample that contained 95.1% empty pollen grains. The size and sex of the lizards which produced the remaining 22 faecal samples are unknown.

The mean percentages of completely empty *Opuntia* and *Tribulus* pollen grains in the faecal samples were  $92.4 \pm 5.4\%$  and  $89.9 \pm 19.8\%$  respectively. In contrast, the percentages of empty pollen grains in samples taken directly from the flowers were only  $4.2 \pm 4.0\%$  for *Opuntia* and  $13.5 \pm 6.4\%$  for *Tribulus*. Contingency table analysis shows that for each pollen species, the mean number of empty pollen grains in the faecal samples was significantly greater than the mean number of empty grains in the flower samples (*Opuntia*: Chi Square = 209.8,  $P < 0.001$ ; *Tribulus*: Chi Square = 468.3,  $P < 0.001$ ). These results show that the exine of both species of pollen is penetrated during passage through the lizard gut (Figure 1).

## DISCUSSION

The results above show that lava lizards on Daphne penetrate the exine of about 90% of the *Tribulus* and *Opuntia* pollen grains they ingest. This ability exceeds that of most birds and equals that of Darwin's finches in Galápagos, and some marsupials in Australia. This ability suggests that Galápagos lizards and finches may have especially efficient digestive tracts for degrading pollen. Alternatively, the exines of *Opuntia* and *Tribulus* pollen may be unusually easy to penetrate. Pollen varies in structure and size between species and *Opuntia* and *Tribulus* pollen may be relatively easy to perforate in comparison with other species of pollen ingested by various animals in similar studies (see Table 1). For instance, pollen from

**Table 2.** Food items of *M. albemarlensis* on Daphne Island. Species were identified from the following sources: Wiggins and Porter (1971) and Black (1974). \* = plant species whose flowers are consumed.

<u>Plant Material</u>	<u>Arthropods</u>
<i>Desmodium glabrum</i>	<i>Aedes taeniorhynchus</i>
<i>Ipomoea linearifolia</i> *	Beetle larvae
<i>Merremia aegyptica</i>	<i>Centruoides exsul</i>
<i>Opuntia echios</i> *	Coccidae sp.
<i>Portulaca howelli</i> *	Diptera spp.
<i>Sesuvium edmonstonei</i> *	Fly larvae
<i>Sida savifolia</i> *	<i>Forcipomyia fuliginosa</i>
<i>Tephrosia decumbens</i> *	<i>Gersteckeria</i> sp.
<i>Tiquilia galapagoa</i> *	Moth spp.
<i>Tribulus cistoides</i> *	<i>Schistocerca melanocerca</i>
	<i>Stomion levigatum</i>
	<i>Stomoxys calcitrans</i>
	<i>Tabanus vittiger</i>
	<i>Thysanura</i> sp.
	<i>Utethesia</i> sp.
<u>Bird Faeces</u>	
<i>Sula dextylata</i>	
<i>Sula nebouxi</i>	
<u>Vertebrates</u>	
<i>Phyllodactylus galapagoensis</i>	
<i>Microlophus albemarlensis</i> young	

**Table 3.** Percentages of full and empty pollen grains found in samples taken from *Opuntia* and *Tribulus* flowers and lizard faeces on Daphne Island.**OPUNTIA**

Total # Grains Counted	FLOWERS		Total # Grains Counted	FAECES	
	% Full	% Empty		% Full	% Empty
144	89.6	10.4	70	14.3	85.7
115	88.7	11.3	293 <sup>1</sup>	12.3	87.7
115	100	0	73	11.0	89.0
113	99.1	0.9	42	4.8	95.2
162	98.8	1.2	48	2.1	97.9
237	97.0	3.0	30	3.3	96.7
146	98.6	1.4	30	6.7	93.3
157	96.8	3.2	153	7.2	92.8
144	93.1	6.9	189 <sup>2</sup>	9.5	90.5
124	96.0	4.0	62	1.6	98.4
			330	19.7	80.3
			95	7.4	92.6
			38	0	100
			185	6.0	94.0
Mean %	95.8	4.2		7.6	92.4
+ - SD	4.0	4.0		7.7	5.4

**TRIBULUS**

Total # Grains Counted	FLOWERS		Total # Grains Counted	FAECES	
	% Full	% Empty		% Full	% Empty
456	81.1	18.9	32	0	100
890	88.5	11.5	55	5.5	94.5
824	74.6	25.4	120	6.7	93.3
818	91.1	8.9	104	1.9	98.1
499	92.0	8.0	41 <sup>3</sup>	0	100
518	94.2	5.8	64 <sup>4</sup>	75.0	25.0
296	78.7	21.3	209	0.5	99.5
923	87.4	12.6	377	8.0	92.0
622	86.7	13.3	153	11.8	88.2
758	91.3	8.7	36	8.3	91.7
			1121 <sup>5</sup>	4.9	95.1
			154	5.2	94.8
			50	4.0	96.0
Mean %	86.6	13.5		10.1	89.9
+ - SD	8.0	6.4		24.2	19.8

<sup>1</sup> = faecal sample from adult male (svl=83mm)<sup>4</sup> = faecal sample from emaciated adult female (svl=66mm)<sup>2</sup> = faecal sample from adult female (svl=64mm)<sup>5</sup> = faecal sample from adult male (svl=85mm) fed *Tribulus* flowers.<sup>3</sup> = faecal sample from adult female (svl=67mm)

*Opuntia* species is larger (100-150  $\mu\text{m}$  diameter) and has a thicker exine (~ 8  $\mu\text{m}$ ) than pollen from *Banksia* species consumed by several birds, bats and marsupials (~ 82  $\mu\text{m}$  diameter, 1.5-4  $\mu\text{m}$  thick), but it also has "windows" in the exine that are only 1  $\mu\text{m}$  thick and may be easy to penetrate. *Tribulus cistoides* pollen has few pores but is small

and has a thin exine (Erdtman 1952, Kapp 1969).

The mechanism for protoplast extraction among pollen consumers is poorly understood (Law 1992). Penetration of the exine is either the result of long passage time through the gut or the direct result of stomach or intestinal enzymes. While the proportion of empty grains

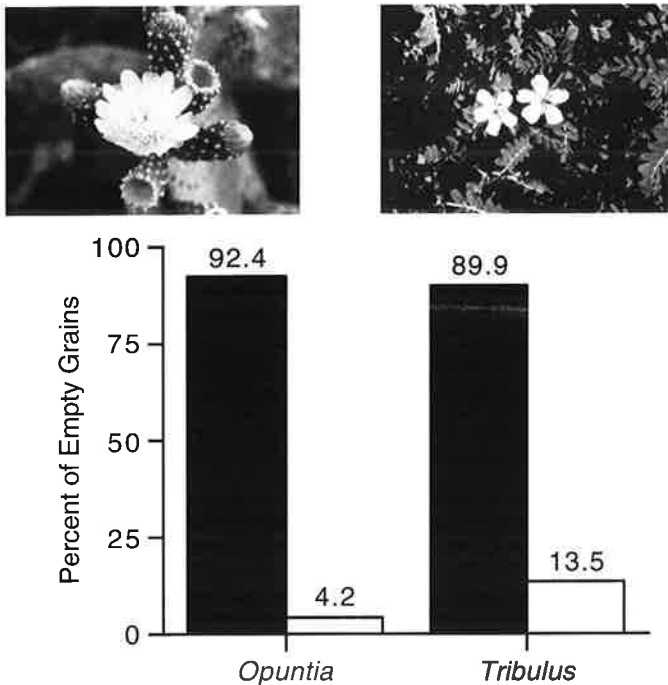


Figure 1. Proportion (%) of empty *Opuntia* and *Tribulus* pollen grains found in faecal (black) and flower (white) samples.

to full grains in the faeces is considered an indicator of digestion (Brice et. al 1989), this index relies on the assumption that once the tough exine is penetrated, the nutrients in the protoplast are assimilated by the animal. Physiological studies of the lava lizard digestive system and detailed chemical analysis of lizard faeces are needed to determine how much of the nutritious protoplast is absorbed and how much is excreted.

Typical values for the contents of pollen are 20% protein, 37% carbohydrates, 4% lipids and 3% minerals and trace elements, but these proportions vary among species (Richardson et al. 1986, Iwanami 1988). Chemical analysis of the nutritional components of *Opuntia* and *Tribulus* pollen is needed to determine if a lizard could satisfy its daily protein requirements by consuming pollen alone. Turner (1984) believes that the marsupials *Tarsipes rostratus* and *Cercartetus nanus* could easily satisfy protein requirements by consuming the total pollen contents of very few *Banksia* flowers.

Lava lizards probably derive a significant portion of energy from flowers in general. Of the eight flower species in their diet (*Sesuvium edmonstonei*, *Portulaca howelli*, *Tephrosia decumbres*, *Tiquilia galapagoa*, *Sida savifolia* and *Ipomoea linearifolia*, in addition to *Opuntia* and *Tribulus*), three (*Opuntia*, *Tiquilia* and *Ipomoea*) bloom during the dry season when arthropods are in short supply. The remaining plants flower shortly after the first rains of the year, usually coinciding with a bloom of arthropods. For instance, in 1991 and 1992 I documented a 100 fold increase in numbers of flies from the dry season (January) to the beginning of the wet season (February–March), and a doubling of arthropod species on Daphne (East 1994).

The minute white inflorescences of *Tiquilia*, which flowers during the dry season, may comprise a significant portion of the diet of juvenile lizards. Juveniles have fewer food choices than larger individuals, being able to feed only on small flies and small flowers (East, 1994). In 1990 and 1991, I saw large numbers of juveniles congregating in patches of the ground-sprawling *Tiquilia*, searching for and consuming flowers. When the patch was denuded of blooms, they moved on to an adjacent patch. Unfortunately, during the study period in 1994, *Tiquilia* was not flowering and I found no pollen grains in the faeces.

*Tribulus*, which flowers during the lizard breeding season, may provide a significant energy source to adult males occupied in territorial defense and courtship. In 1991, adult males allocated little time to chasing mobile prey during weeks of intense territorial defense and courtship, but consumed large numbers of *Tribulus* flowers instead. In contrast, breeding females in the same area pursued moths attracted to the flowers but ignored the flowers themselves. In 1994 these moths were absent and both adult males and females fed on significant quantities of *Tribulus* flowers (East 1994).

### Pollen Acquisition

Lizards obtain pollen by various means, depending on the plant species. Unlike *M. pacificus* on Pinta (Schluter 1984), *M. albemarlensis* on Daphne rarely climbs *Opuntia* bushes to reach the flowers. *M. pacificus*, a larger lizard, is able to tear petals directly from the flowers, an almost impossible task for the smaller *M. albemarlensis* on Daphne. Furthermore *Opuntia* bushes on Daphne are covered with many more spines than the *Opuntia galapagoa* trees on Pinta, hindering movement among the pads. Rather, the lizards on Daphne obtain *Opuntia* pollen opportunistically, via a special relationship with *Geospiza scandens*. When the finches visit the flowers, to feed on the nectar and pollen themselves, lizards congregate underneath and chase after the pollen-laden stamens and petal fragments that shower down. Falling yellow petals attract lizards from meters away. Alternatively, recently fallen pads with open flowers, and flowers close to the ground are targeted by the largest lizards (adult males) which rip out the stamens.

*Tribulus* and *Portulaca* are low growing plants with flowers that are small and easily accessible. The flowers are literally attacked from the middle; the lizard grabs the flower from the base of the stigma and pulls back with a sudden head movement. Often the entire flower head comes off and is consumed whole; otherwise portions are torn off one at a time.

The flowers of *Ipomoea*, an abundant plant on Daphne, are favored by the Galápagos Dove, *Zenaida galapagoensis* (Grant and Grant 1979). When a dove begins tearing at the petals, lizards in the vicinity run to pick up dropped fragments. However, pollen is probably rarely ingested as only outer petal fragments are eaten and unlike *Opuntia* petals, they are not dusted with pollen. Two *Ipomoea* pollen



grains were found in two faecal samples but both were full (undigested).

*Sida*, *Tephrosia*, *Sesuvium* and *Tiquilia* flowers are all very small and are consumed whole by the lizards. While *Sida* and *Tephrosia* flowers are always scarce, *Sesuvium* and *Tiquilia* flowers can be seasonally abundant.

I should note that the absence of *Sesuvium*, *Portulaca*, *Sida*, *Tephrosia* and *Tiquilia* pollen in the faeces is attributed in large part to sampling bias. Fresh faeces are hard to find due their small size and camouflage with the ground. They are also often produced under low lying vegetation and in cracks in the rocks and are thus hidden or inaccessible. I found most faeces in open rocky areas with scattered *Opuntia* bushes and patches of *Tribulus* plants. Areas with dense mixed vegetation were harder to sample.

### Ecological Implications of Pollen Digestion Among Lizards

Herbivory in lizards is generally considered a poor alternative to carnivory as plant material contains less energy than arthropods (Pough 1973) and often requires specialized anatomical structures such as modified dentition, endosymbiotic microorganisms and a relatively large body size (Szarski 1962, Zimmerman and Tracy 1988). Pough (1973) showed that large lizards exhibit a greater degree of herbivory than small lizards and suggested that while herbivory enables large lizards to satisfy their greater caloric demands, small lizards are unable to acquire equal amounts of energy from plant material because it passes through their shorter gut more rapidly. More recent studies, however, show that herbivory is more widespread among small reptiles (Rocha 1989, van Sluys 1993) and more energy and nutrient rewarding (Mautz and Nagy 1987, Bjorndal and Bolten 1992) than previously thought. While arthropods contain proportionately more usable energy and protein than do plants, some parts of plants have greater nutrient stores than others, pollen being one example (Faegri and van der Pijl 1971, Stanley and Linskens 1974). Troyer (1984) found that young herbivorous Iguana maximize their protein intake by selecting immature leaves of *Lonchocarpus pentaphyllus* which contain more protein and less fiber and lignin than do more mature leaves. Ostrom (1963) noted that most plant-eating reptiles have limited masticatory capabilities and that in nearly every herbivorous diet the preferred plant tissues, fruits and flowers, were soft and easy to digest. Frugivory is common in lizards (Racine and Downhower 1974, Schluter 1984, Iverson 1985, Whitaker 1987, 1987a) and sugary fruits, nectar, flowers and young leaves can provide sufficient quantities of carbohydrates and fats (Golley 1961, 1969, Howell 1974). This study introduces the possibility that pollen may supplement or fully provide the nitrogen components necessary for the maintenance and growth of lizards during times when other protein sources, such as arthropods, are scarce.

While the ability of lava lizards on Daphne to digest pollen may merely be a function of a strong digestive system adapted for unrelated reasons, it may alternatively be an adaptation to island conditions where arthropods are in fluctuating supply and pollen offers an alternative source of protein, it may merely be. Replications of this study are needed on other lizard species in both Galápagos and other parts of the world to determine if pollen digestion in lizards is unusual or common place. Pollen should not be over-looked as a potential source of protein in future studies of lizard feeding behavior.

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## SIZE-DEPENDENT PREDATION BY FERAL MAMMALS ON GALÁPAGOS *OPUNTIA*

By: David J. Hicks and André Mauchamp

Oceanic islands typically possess biotas with high susceptibility to damage by introduced plants and animals (Schofield 1989, Loope et al. 1988). Change in the flora of the Galápagos Islands is a well-documented example of such damage. On most of the larger islands, native vegetation has been significantly altered in composition by feral mammalian herbivores (Hamann 1984, Schofield 1989, Loope et al. 1988).

Previous studies of herbivory by introduced mammals in Galápagos have been concerned primarily with the species of plants consumed, and with effects on vegetation structure (e.g. Calvopiña and de Vries 1975, de Vries and Calvopiña 1977). However, little is known about how food plants are selected within palatable species.

In predator-prey interactions involving animal species, many cases are known in which predation is size-dependent (e.g. Paine 1976). Frequently, both small and large prey individuals are consumed disproportionately rarely by predators; small individuals because they do not provide sufficient food rewards, and large ones because they are too difficult to capture or consume. Although seed size clearly influences food consumption by granivores (e.g. Grant 1986), examples of the effect of whole plant size on rates of herbivory are rare.

In this paper we describe size-dependent predation by feral goats (*Capra hircus* L.) and burros (*Equus asinus* L.) on the tree cacti *Opuntia echios* var. *gigantea* Howell and *O. galapageia* var. *galapageia* Hensl. in the arid zone of Galápagos. (Hereafter, varietal epithets of these *Opuntia* taxa will be omitted). These animals damage cacti by biting into the cladodes or through the bark of the trunk to reach the pulp. The only large native herbivores, land iguanas (*Conolophus subcristatus* and *C. pallidus*) and giant tortoises (*Geochelone elephantopus*), eat fallen pads and fruits, but are not known to damage trunks in this way (Carpenter 1969, Rodhouse et al. 1975, Christian et al. 1984). As suggested by Snell et al. (1994), introduced mice can also be a threat to *Opuntia* populations because they consume the roots and may accelerate mortality.

*Opuntia echios* was studied on Santa Cruz Island, in a zone where introduced herbivores are typically uncommon, and the vegetation is relatively stable (Eliasson 1982; Hamann 1984). *O. galapageia* was studied on Santiago Island, where large populations of feral goats and burros are present and have caused significant damage to the native vegetation (Schofield 1989, Hamann 1993). Goat populations are very high, estimated at 60,000 to 80,000 individuals on the 572 km<sup>2</sup> island (unpublished analysis by W. Pittroff, based on data of L. Calvopiña).

### STUDY SITE AND METHODS

*Opuntia echios* was studied on Santa Cruz, about 0.7 km north of the Charles Darwin Research Station. The approximate elevation is 30 m. The vegetation is low (less than 2 m tall, with the exception of occasional cacti), with about 80% total plant cover. *O. echios* was common at the site and reached a maximum height of 5 m. Dominant plants were *Cordia leucophlyctis*, *Cordia lutea*, *Prosopis juliflora*, *Acacia rorudiana*, *Ipomoea triloba*, and *Lantana peduncularis* (Wiggins and Porter 1971). Burro droppings were found, but no signs of goats were encountered. The droppings and bites on *Opuntia* trunks appeared to be at least several months old.

*Opuntia galapageia* was studied in the north-central part of Santiago, near La Bomba. This site was also in the arid zone, at an elevation of about 2 to 10 m. Vegetation dominants were *Bursera graveolens*, *Castela galapageia*, *Clerodendron molle*, and *Lantana peduncularis*. Although some *Bursera* trees reached 4 m height, this site was quite open, with vegetation covering only about 30%. The very high frequency of droppings and sightings of animals suggest an abundance of goats and burros. Much evidence of recent damage to *Opuntia* plants, from near ground level to about 1.8 m height, was found, and prob-

**Table 1.** Relationship between spine cover of *Opuntia* and probability of damage to the trunk by feral goats and donkeys. The number of damaged plants expected was calculated on the assumption that the same proportion of plants would be damaged in each size class. Obs = observed, Exp = expected, N = number of plants examined, % = percent damaged.

Spine cover	Number of Damaged Plants			
	Obs	Exp	N	%
<i>O. echios</i> , Santa Cruz				
Heavy	0	5.6	21	0
Moderate	8	5.1	19	42
Light	22	19.3	75	29
(Chi Square = 33.1, p < 0.001)				
<i>O. galapageia</i> , Santiago				
Heavy	5	12.9	76	7
Moderate	7	4.6	27	26
Light	8	2.5	15	53
(Chi Square = 21.5, p < 0.001)				

ably represents a combination of burro and goat attacks. It was not possible to visually distinguish between burro and goat damage.

In both areas, *Opuntia* plants with heights of  $\geq 2$  m were surveyed. This cutoff was chosen because these plants begin to form definite terete trunks and to produce flowers at about this size. Furthermore, plants  $< 2$  m height showed no bite damage by large animals. We recorded the diameter of the trunk at a height of about 0.5 m, the degree to which spines covered the trunks ("heavy" = 75-100% cover by spines, "moderate" = 25-75% cover, and "light" =  $< 25\%$  cover), and the presence of bites on the trunk and cladodes. We also recorded the diameter of plants killed by bites. On Santa Cruz, data were collected within an area of approximately 0.5 ha. On Santiago we walked a circuit of about 2 km length, recording data on all cacti of appropriate height.

Statistical tests and calculations were done by the program SPSSPC. Values reported are means  $\pm$  standard deviations.

## RESULTS

At the Santa Cruz site, 30 of 115 living plants (26%) displayed burro damage to the trunk; none had damage to cladodes. On Santiago, 20 of 118 living plants (17%) had trunk damage, 21 (18%) had cladode damage, and 2 (2%) had both.

On Santa Cruz, plants with heavy spine cover had a mean trunk diameter of  $12.1 \pm 2.1$  cm ( $n = 21$ ), versus  $15.7 \pm 2.9$  cm ( $n = 19$ ) for plants with moderate spine cover and  $20.4 \pm 5.5$  cm ( $n = 75$ ) for those with light cover. These differences were statistically significant (Kruskal-Wallis test,  $P < 0.01$ ). Diameter also varied significantly with spine class at the Santiago site, although differences were smaller. Here, plants with heavy spines had a mean diameter of  $17.6 \pm 4.3$  cm ( $n = 18$ ), those with moderate spines  $21.8 \pm 3.9$  cm ( $n = 30$ ) and those with light spines  $20.8 \pm 5.0$  cm ( $n = 82$ ). Again, differences were statistically significant (Kruskal-Wallis test,  $p < 0.02$ ).

**Table 2.** Relationship between trunk spine cover of *Opuntia* and probability of damage to cladodes by feral goats and donkeys, for the Santiago site only. Obs = observed, Exp = expected, N = number of plants examined, % = percent damaged.

Spine cover	Number of Damaged Plants			
	Obs	Exp	N	%
Heavy	12	13.5	76	16
Moderate	5	4.8	27	19
Light	4	2.7	15	27

(Chi Square = 1.03,  $p = 0.60$ )

**Table 3.** Relationship between *Opuntia* trunk diameter and probability of damage by feral goats and donkeys. Plants with heavy spine cover are omitted from this analysis. Obs = observed, Exp = expected, N = number of plants examined, % = percent damaged.

### *O. echinos*, Santa Cruz

Diameter class	Number of Damaged Plants			
	Obs	Exp	N	%
$< 20$ cm	24	18.7	58	41
$> 20$ cm	6	11.3	35	17

(Chi Square = 5.9,  $p = 0.02$ )

### *O. galapageia*, Santiago

$< 20$ cm	11	10.4	29	38
$> 20$ cm	4	4.6	13	31

(Chi Square = 0.20,  $p = 0.65$ )

Presence or absence of damage to the trunk was strongly related to the degree of spine coverage for both sites (Table 1). For the Santiago site, there was no relationship between cladode damage and the degree of spine cover (Table 2).

When plants with heavy spines were omitted from the analysis, a significant relationship between trunk diameter and damage was detected for the Santa Cruz site, with plants having a diameter  $> 20$  cm experiencing less frequent damage than expected. However, we found no relation between size and damage to cacti at the Santiago site (Table 3).

Bite-killed plants were very common on Santiago (40 of 158, or 25%). The diameter of dead plants ( $17.8 \pm 4.6$ ,  $n = 40$ ) averaged a bit smaller than those of live plants ( $19.3 \pm 4.7$ ,  $n = 118$ ), but the difference was not significant (Mann-Whitney test,  $p = 0.10$ ). There were insufficient numbers of dead plants (3 of 118, or 3%) to perform statistical tests for the Santa Cruz site.

## DISCUSSION

It is clear that adult *Opuntia* plants are severely damaged by feral animals. Although Eliasson (1968) and Weber (1971) noted damage to trunks by goats, most previous discussions have emphasized trampling or consumption of small plants (van der Werff 1982; Schofield 1989). We did observe a few small plants (diameter  $\leq 8$  cm) on Santiago that may have been uprooted by feral animals, but this was infrequent in the populations studied. In contrast, damage to trunks and cladodes of large plants was very frequent.

Repeated attacks to an *Opuntia* can girdle the trunk and kill the plant. Cladodes of both *Opuntia* species are capable of rooting after such an event. However, vegetative reproduction from fallen cladodes seems to be very rare in *O. galapageia* on Santiago. This is probably because the cladodes of older plants of this species have bristly, rather soft, spines rather than the long, sharp spines found on younger plants (Wiggins and Porter 1971). Fallen cladodes of older plants are quickly consumed by animals, and usually do not survive long enough to take root.

The selection of cacti as food by feral mammals is clearly size-dependent. Damage was dependent on trunk size, with both small and large diameter stems avoided. The probable reason for avoidance of small trunks is the dense armature of spines. In the Santa Cruz population of *O. echios*, large stems are probably avoided because they exceed the gape size of the animals.

The absence of a significant size effect in *O. galapageia* may be due to differences in trunk size. *O. echios* has a maximum diameter of at least 60 cm, while *O. galapageia* trunks larger than 32 cm were not found in this study. In the study areas, 22% of *O. echios* were > 25 cm diameter, while only 8% of *O. galapageia* were this large. Thus, failure to find a size effect in the latter species may reflect the rarity of large trunks. Another possible explanation for the lack of a size effect is greater herbivore pressure. As *Opuntia* trunks age, patches without spines develop. On Santiago, we saw numerous cases where bite damage occurred in small spineless areas. On Santa Cruz, where food sources other than cacti are common, bites occur mostly on trunks with large patches devoid of spines, or those without spines.

The results of this study have important conservation implications. In both *O. echios* and *O. galapageia*, reproduction is size-dependent. The average diameter of flowering *O. echios* is 26 cm, and that of flowering *O. galapageia* 21 cm. In both species there is a positive correlation between trunk diameter and levels of fruit production (D. Hicks and A. Mauchamp, unpublished data). Damage to medium- or large-diameter individuals could thus constitute a bottleneck in survivorship that prevents plants from reaching reproductive size. In the long term, predation may significantly reduce recruitment to *Opuntia* populations, even though small cacti may not be directly damaged. This appears to be especially crucial in the Santiago study area, where 60% of large *O. galapageia* were damaged or killed by animals. The elimination of reproductive individuals is already occurring on Santiago. In a set of 12 plots from 2 to 135 m elevation, we found only 5.5% of *O. galapageia* individuals to be reproducing sexually. In a similar study on Santa Cruz, 19.2% of *O. echios* were reproductive (D. Hicks and A. Mauchamp, unpublished data).

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## GEOGRAPHICAL CHARACTERISTICS OF THE GALÁPAGOS ISLANDS

By: Heidi M. Snell, Paul A. Stone, and Howard L. Snell

### INTRODUCTION

People interested in science or conservation in Galápagos often ask "How big and isolated is an island?" These two questions form the basis of the celebrated theory of island biogeography (MacArthur and Wilson 1967). This theory proposes that the size and isolation of islands can predict aspects of their biotic communities such as the numbers and types of species. Elements of the theory have been verified for a wide range of island archipelagos throughout the world, including Galápagos (Simberloff and Wilson 1969, Johnson and Raven 1973).

There are no complete systematic accounts of characteristics of the islands within the Galápagos Archipelago. Partial reviews of island characteristics have been published (Wiggins and Porter 1971, Black 1973). However, both of these sources concentrated on the larger islands in the archipelago and used potentially inaccurate methods, which, while they were the best available at the time, have since been superseded. These reviews also were published before the availability of highly accurate Ecuadorian navigational charts of the Galápagos, which have improved the resolution of measurements of island areas and isolations. In addition, these summaries disagreed substantially on the areas of several islands. We therefore decided to present this brief review which includes characteristics of many islands previously not quantified. These data have been compiled as part of our research on the biological diversity of the Galápagos Archipelago. While we will present the results of that research as a series of correlations with these data, we felt that many people interested in the Galápagos Islands would appreciate access to this review of the islands prior to our publication of their correlates with diversity. This summary includes all islands known to us in the Galápagos, 121 of them! We have purposefully not included altitude as a characteristic. Unfortunately, altitudes measured by a variety of methods are not comparable. We don't feel that our current altitudinal data represent an improvement over previously published values. We expect to change that in the future.

### METHODS

We define an island as any permanently isolated land that is vegetated with terrestrial plants other than mangroves. Occasionally, we have included islands that we suspect are vegetated without having visually surveyed them. We measured area and isolation using published maps, aerial photographs, and our own measurements

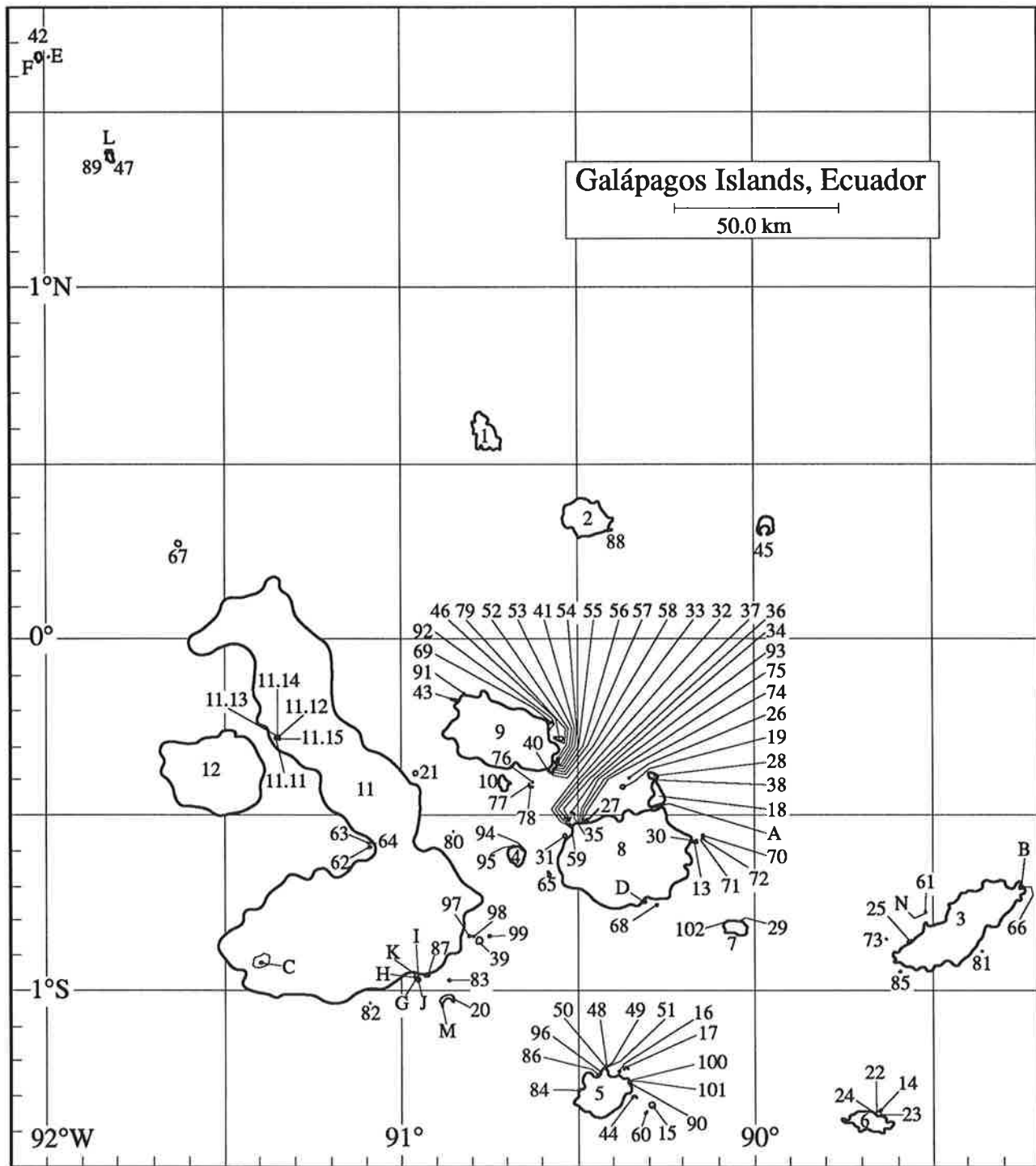
with receivers of positional signals from the Global Positioning System (GPS). We sometimes used published accounts of island areas, especially for large or well-studied islands (Wiggins and Porter 1971; Black 1974; Snell et al. 1988; Cayot et al. 1994). Table 1 provides the specific source for each characteristic we measured.

We used two measures of isolation that we felt addressed different aspects of isolation. First, we measured the distance from the center of an island to the geographical center of the archipelago. The center of the archipelago was determined by simultaneously measuring the distance from a proposed central point to all 121 islands. The mean of those distances was simultaneously calculated and displayed. We modified the position of the proposed central point until the mean distance was at its minimum. The proposed point at that time was as close to all islands as possible, a situation we defined as the center of the archipelago. The isolation distances were then calculated as the hypotenuses of right triangles formed by taking the differences in latitude and longitude of the center of each island and the center of the archipelago as the right sides.

Second, we measured the distance from an island to its nearest large neighbor, regardless of ocean currents or topography, as proximate isolation. We usually measured proximate isolation directly from charts using calipers. We classified islands as either small or large, and for small islands we always measured the distance to the nearest large island. For large islands, we measured the distance to the nearest larger island (the largest island, Isabela, had no measure of proximate isolation). We believe these conventions maximized our chance of measuring the distance that potential colonists would have to travel in order to colonize a particular island. An interesting alternative would be to measure to the nearest older island. However, sufficiently accurate estimates of the ages of the 121 islands treated here were not available to us.

We measured area by scanning an image of the island traced from navigational charts or aerial photographs into a Macintosh computer. The scanned image was imported as a PICT file into Canvas 3.03, a drawing program. In Canvas, the island area was measured using a freehand tool traced around the perimeter.

We followed three rules when calculating areas and isolation distances. First, size and isolation were measured at the estimated high-tide coastlines of islands. Second, size and isolation were measured using the largest scale map or photograph available. Finally, if an aerial photograph and a map of similar scale revealed different values for the same measurement, we used the photograph.



**Figure 1.** Relative positions of the islands of the Galápagos Archipelago.

These positions were plotted by converting the positions from Table 1 to a linear X(longitude) - Y(latitude) coordinate system. Those data were then imported into Cricket Graph III and plotted as a scatter plot with the points labelled with the codes in Table 1. That plot was then imported as a background layer in Freehand 5.0. A previously developed map of most of the archipelago was opened as another layer. By resizing the map until the centers of the islands corresponded with the plotted points in the background layer we were able to exactly position the many small islands not correctly plotted on the previous map. Due to the conversion of the positions to a linear scale some small errors in position may exist at the extremes of the archipelago. While the islands depicted here are accurate in their relative positions, we caution against the use of their outlines for area measurements. Because of variations in scale of the various scanned images, they could not always be used to develop the shapes of the islands on this map.



Positions of the islands were determined from our own measurements via GPS receivers when possible. In those instances we used the WGS 84 Datum for corrections. Otherwise we used the largest scale Ecuadorian navigational chart (IOA) available. If an Ecuadorian chart was not suitable we used British Admiralty charts (BA). Finally if Ecuadorian and British Admiralty charts were not suitable, we used United States charts from the Defense Mapping Agency (DMA). We found that the IOA charts were superior to all others for positional accuracy, the BA charts second, and the DMA charts third.

Many of the islands included here have never been described before. Thus, names for them are lacking. It was not our purpose to present a review of names, which are in a confusing disarray (Woram 1989). For that reason, we have used names commonly applied by the staff of the Charles Darwin Research Station, ourselves, or other residents of Galápagos. To avoid confusion we have included the positions of all islands in Table 1 and a coded map indicating relative positions as Figure 1.

## RESULTS AND DISCUSSION

Table 1 presents the size, isolation, and position for 121 islands of the Galápagos Archipelago. This is an increase of approximately 40% in the number of islands previously recorded from the Galápagos (45+ [Wiggins and Porter 1971], 87 [Black 1973], 59+ [Jackson 1993]). Many of the previous accounts grouped islets such as the Marielas, Rocas Beagle, Guy Fawkes, Rocas Bainbridge, and Rocas Gordon. Those five groups actually contain 21 islets. However, a number of the islets included here represent complete additions to the published literature (although not new "discoveries" as the Galápageños know of every rock). For example, Islotes las Cuevas, Roca Rata, Islotes Caleta Tiburon, Islote Oeste, Islote Mao, and others have no published recognition known to us.

The center of the Galápagos Archipelago, based upon the 121 islands in Table 1, is located at 0° 32.22' S and 90° 31.26' W. This is near the NW corner of Conway Bay, Santa Cruz and is closest (0.5 km) to Islote Punta Bowditch Sur (33 on the map in Figure 1). It is fun to note that a small blow-hole occurs on the islet very close to this site. We refer to the blow-hole as "The Center of the Galápagos." Previous analyses using the distance from the center of the archipelago as a measure of isolation have assumed Santa Cruz as the center (Johnson and Raven 1973). The different techniques of identifying the archipelago's center yield strikingly different estimates of isolation. Our center yields measures of isolation that are greater than previous estimates by an average of 23.5 km. Expressed as a percentage of the previous value of isolation the average difference is 536%. Unfortunately, the differences are not consistent (ranging from 3 to 6500%). Thus, the effect of the different measures will not be uniform when isolation is used in analyses of patterns of distribution.

Most of the variation in the differences comes from our use of a point and the previous use of an island as the center. Using an island as the center allows islands that are separated by as much as 50 km to have "distances from the center of the archipelago" that are less than 1 km (Eden and Las Plazas, Johnson and Raven 1973).

Previously reported areas for six islands (Darwin, Wolf, Isla Lobos, Mosquera, Roca Redonda, Eden) differed by more than 20% (Wiggins and Porter 1971, Black 1973). For all of these islands except Darwin and Wolf we made an independent measure of island area. In those four cases our measurement of island area was closer to and within 20% of the value reported by Black (1973). Therefore, for islands whose area we did not measure but were measured by both Wiggins and Porter (1971) and Black (1973), we used the value from Black (1973). For all islands except Darwin and Wolf, choosing the Black (1973) value over the Wiggins and Porter (1971) value is a convention since the two estimates are very similar. However, the true areas of Darwin and Wolf remain in doubt. No good maps of these two islands exist, and the estimates of Black (1973) are less than 1/2 those of Wiggins and Porter (1971). Unfortunately, we cannot resolve this discrepancy in the present study.

The data in Table 1 are the most comprehensive and current list available, but this list will continually need amending. First, we are not certain this list includes every island in the archipelago. There may be scattered and isolated small islands near unexplored coasts of remote islands such as Pinta or Isabela that we missed. We also may have inadvertently included islands that are wave-washed or not vegetated. Finally the sizes, and to a lesser extent the isolations, depend on the accuracy of the published maps, which may often be imperfect. We encourage readers to point out any mistakes they uncover.

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**Table 1.** Characteristics of the Galápagos Islands.

Map Code <sup>1</sup>	Island Name <sup>2</sup>	Position	Pos. Ref. <sup>3</sup>	Area (ha)	Area Proximate Ref. <sup>3</sup>	Isolation (m)	Isolation From	Isol. Ref. <sup>3</sup>	Dist. to Center (km)
11	<b>Isla Isabela</b>	0°25'30"S, 91°7'W	37	458812.0	1				67.4
C	Islote Cráter Cerro Azul	0°55'30"S, 91°24'W	37	0.600	36	500	Isabela	36	106.8
82	Roca Union	1°2'10.5"S, 91°5'28"W	20	0.050	36	2850	Isabela	20	84.2
83	Roca Viuda	0°58'19"S, 90°52'9"W	20	0.684	20	4389	Isabela	20	61.9
20	Isla Tortuga	1°1'21.5"S, 90°52'11.5"W	20	129.896	20	6780	Isabela	20	66.4
M	Islote Tortuga Oeste	1°1'36"S, 90°52'46"W	40	3.565	20	496	Tortuga	20	67.4
I	Islote Camino del Turismo (Villamil)	0°58'11"S, 90°57'31"W	20				Isabela		68.4
G	Islote Faro (Villamil)	0°57'47"S, 90°57'44"W	20				Isabela		68.2
H	Islote Fondiadero (Villamil)	0°57'49"S, 90°57'39"W	20				Isabela		68.1
K	Islote Muelle (Villamil)	0°57'54"S, 90°57'25"W	20				Isabela		67.9
J	Islote Villamil Sureste	0°58'22"S, 90°57'12"W	20				Isabela		68.2
87	La Lobería	0°57'37"S, 90°55'36"W	20	0.200	36		Isabela	36	65.1
98	Islote Cuatro Hermanos #2	0°50'41"S, 90°47'54"W	40	30.405	23	3626	Isabela	23	46.0
99	Islote Cuatro Hermanos Este	0°50'42"S, 90°44'55"W	40	7.264	23	8838	Isabela	23	42.6
97	Islote Cuatro Hermanos Oeste	0°50'39"S, 90°48'30"W	40	20.416	23	2701	Isabela	23	46.7
39	Islote Cuatro Hermanos Sur	0°51'30"S, 90°46'30"W	40	72.928	23	6154	Isabela	23	45.5
80	Roca Blanca	0°32'45"S, 90°51'21"W	40	0.300	2	7366	Isabela	28	37.2
21	Isla Cowley	0°22'56"S, 90°57'39"W	28	3.500	36	3214	Isabela	28	51.8
67	Roca Redonda	0°16'30"N, 91°37'35"W	37, 42	4.311	24	24060	Isabela	24	152.4
11.11	Islote Cráter Beagle #1	0°16'59.6"S, 91°21'8.8"W	44	1.562	18	262	Isabela	18	96.6
11.12	Islote Cráter Beagle #2	0°16'46.5"S, 91°20'59.4"W	44	1.697	18	487	Isabela	18	96.4
11.13	Islote Cráter Beagle #3	0°16'29"S, 91°20'53"W	18	0.067	18	393	Isabela	18	96.4
11.14	Islote Cráter Beagle #4	0°16'26.5"S, 91°20'53"W	18	0.032	18	364	Isabela	18	96.4
11.15	Islote Cráter Beagle #5	0°17'00.4"S, 91°20'52.8"W	44	0.096	18	321	Isabela	18	96.1
64	Islote Marielas Este	0°35'28"S, 91°5'17"W	19	0.067	19	738	Isabela	19	63.3
63	Islote Marielas Norte	0°35'31"S, 91°5'19.5"W	19	0.242	19	812	Isabela	19	63.4
62	Islote Marielas Sur	0°34'43.5"S, 91°5'18"W	19	1.253	19	848	Isabela	19	63.2
12	<b>Isla Fernandina</b>	0°22'0"S, 91°31'20"W	37	64248.0	1	4016	Isabela	18	112.9
8	<b>Isla Santa Cruz</b>	0°37'0"S, 90°21'0"W	37	98555.0	1	27600	Isabela	6	21.0
68	Isla Caamaño	0°45'21"S, 90°16'34"W	15	4.500	15	1287	Santa Cruz	15	36.5
D	Islote Devine	0°45'9"S, 90°18'22"W	15	0.300	36	200	Santa Cruz	36	33.8
13	Isla Plaza Sur	0° 34'56.3"S, 90°9'57.0"W	13	11.9	3	302	Santa Cruz	13	39.8
30	Isla Plaza Norte	0°34'36"S, 90°9'32"W	13	8.844	13	652	Santa Cruz	13	40.5
71	Roca Gordon Central	0°33'51.5"S, 90°8'27.5"W	13	0.259	35	2840	Santa Cruz	35	42.3
70	Roca Gordon Este	0°33'48"S, 90°8'22"W	13	2.912	35	2990	Santa Cruz	35	42.5
72	Roca Gordon Oeste	0°33'55.5"S, 90°8'26.5"W	13	0.828	35	2786	Santa Cruz	35	42.4
26	Isla Daphne Chica	0°23'30"S, 90°20'56"W	37	7.958	10	10520	Santa Cruz	10	25.0
19	Isla Daphne Major	0°25'11"S, 90°22'12"W	37	33.022	10	7600	Santa Cruz	10	21.2
27	Islote Venecia	0°31'00.6"S, 90°28'29.1"W	44	13.279	4	30	Santa Cruz	4	5.6
74	Islote Caleta Tiburon Norte	0°31'10.6"S, 90°28'35.2"W	44	0.137	4	102	Santa Cruz	4	5.3
75	Islote Caleta Tiburon Sur	0°31'13.9"S, 90°28'35.0"W	44	0.104	4	29	Santa Cruz	4	5.3
93	Roca Rata	0°31'16.6"S, 90°29'6.2"W	44	0.035	36	40	Santa Cruz	36	4.4
35	Islote Guy Fawkes Este (2nd smallest)	0°29'48.5"S, 90°30'46"W	26	1.219	31	3448	Santa Cruz	31	4.6
34	Islote Guy Fawkes Norte (smallest)	0°29'45.2"S, 90°30'53.6"W	44	0.235	31	3870	Santa Cruz	31	4.6
37	Islote Guy Fawkes Oeste (largest)	0°30'45"S, 90°31'39"W	44	3.402	31	2131	Santa Cruz	31	2.8
36	Islote Guy Fawkes Sur (2nd largest)	0°30'48"S, 90°31'33"W	28	3.294	31	2343	Santa Cruz	31	2.7

Map Code <sup>1</sup>	Island Name <sup>2</sup>	Position	Pos. Ref. <sup>3</sup>	Area (ha)	Area Proximate Ref. <sup>3</sup>	Isolation (m)	Isolation From	Isol. Ref. <sup>3</sup>	Dist. to Center (km)
59	Islote Punta Bowditch Este	0°31'56"S, 90°30'55"W	26	0.346	31	113	Santa Cruz	31	0.8
32	Islote Punta Bowditch Norte	0°31'57.7"S, 90°31'1.7"W	44	2.918	31	272	Santa Cruz	31	0.7
33	Islote Punta Bowditch Sur	0°32'5.6"S, 90°31'00.8"W	44	1.511	31	184	Santa Cruz	31	0.5
31	Isla Eden	0°33'41.0"S, 90°32'11.2"W	44	23.020	34	293	Santa Cruz	34	3.2
65	Isla Sin Nombre	0°40'0"S, 90°35'0"W	37	7.529	23	4677	Santa Cruz	23	16.0
4	<b>Isla Pinzón</b>	0°36'30"S, 90°39'57"W	28	1815.0	1	10399	Santa Cruz	28	17.9
95	Islote Dumb	0°35'22"S, 90°41'0"W	28				Pinzón		19.0
94	Islote Onan	0°35'47"S, 90°39'10.5"W	28	0.060	36	40	Pinzón	36	16.1
7	<b>Isla Santa Fé</b>	0°49'0"S, 90°3'30"W	37	2413.0	1	16653	Santa Cruz	16	60.1
29	Islote Santa Fé	0°48'13.3"S, 90°2'15.8"W	44	0.671	36	17	Santa Fé	36	61.3
102	Islote Noroeste de Santa Fé	0°48'18.3"S, 90°5'13.6"W	44	0.070	36	70	Santa Fé	36	56.7
18	<b>Isla Baltra</b>	0°25'30"S, 90°16'30"W	12	2619.6	10	361	Santa Cruz	11	30.0
A	Islote de Canal Sur	0°28'54"S, 90°17'26"W	11	0.349	11	64	Baltra	11	26.3
38	Islote Mosquera	0°24'4"S, 90°16'33"W	12	4.626	12	406	Baltra	12	31.1
28	Isla Seymour Norte	0°23'30"S, 90°17'0"W	12	183.887	12	1464	Baltra	12	31.0
5	<b>Isla Floreana</b>	1°17'0"S, 90°26'0"W	37	17253.0	1	49200	Santa Cruz	6	83.5
60	Islote Watson	1°20'41"S, 90°18'31"W	22	3.050	22	8012	Floreana	22	92.8
15	Isla Gardner por Floreana	1°19'52"S, 90°17'20"W	22	81.174	22	7970	Floreana	22	91.9
44	Isla Caldwell	1°18'15.5"S, 90°20'19"W	22	22.837	22	2700	Floreana	22	87.6
90	Islote Ayora	1°16'16"S, 90°21'2"W	22	0.500	36	600	Floreana	36	83.7
101	Islote Las Cuevas Este	1°15'37"S, 90°21'35"W	22	0.130	36	80	Floreana	36	82.3
100	Islote Las Cuevas Oeste	1°15'35"S, 90°21'39.5"W	22	0.100	36	50	Floreana	36	82.3
17	Isla Enderby	1°13'12.5"S, 90°21'42"W	22	19.297	22	2429	Floreana	22	77.9
16	Islote Campéon	1°14'7"S, 90°23'8"W	22	9.508	22	733	Floreana	22	79.0
50	Islote Corona del Diablo Oeste	1°12'48.5"S, 90°25'16"W	17	0.070	25	457	Floreana	25	76.0
48	Islote Corona del Diablo Grande	1°12'43"S, 90°25'14"W	17	0.449	25	500	Floreana	25	75.8
49	Islote Corona del Diablo Central	1°12'44"S, 90°25'14"W	17	0.020	36	20	C. del Diablo G.	36	75.9
51	Islote Corona del Diablo Este	1°12'48"S, 90°25'14"W	17	0.040	36	100	C. del Diablo G.	36	76.0
86	Islote Las Bayas Grande	1°13'25.5"S, 90°26'28"W	17	2.070	25	103	Floreana	25	76.8
96	Islote Las Bayas Pequeña	1°13'29"S, 90°26'25"W	17	0.145	25	94	Floreana	25	76.9
84	La Botella	1°17'13.5"S, 90°29'46"W	17			299	Floreana	17	83.4
3	<b>Isla San Cristóbal</b>	0°48'30"S, 89°25'0"W	37	55808.6	1	66600	Santa Cruz	6	126.4
85	Roca Ballena	0°56'44"S, 89°35'22"W	43			1087	San Cristóbal	21	113.0
81	Roca Este	0°53'21"S, 89°21'33"W	43			2434	San Cristóbal	21	134.9
66	Islote Pitt (offshore)	0°42'14.3"S, 89°14'54.3"W	44	0.400	36	622	San Cristóbal	21	142.6
B	Islote Pitt (nearshore)	0°41'55"S, 89°15'5"W	21	0.500	36	41	San Cristóbal	21	142.2
61	Leon Dormido	0°46'26"S, 89°31'0"W	8	5.021	8	4608	San Cristóbal	8	114.7
N	Leon Dormido Pequeña	0°46'31"S, 89°30'59"W	8	0.975	8	4500	San Cristóbal	8	114.7
25	Isla Lobos	0°51'25.3"S, 89°33'51.8"W	44	6.666	32	162	San Cristóbal	32	112.1
73	Roca Dalrymple	0°51'9"S, 89°37'28.5"W	7	0.800	2	3933	San Cristóbal	7	105.6
6	<b>Isla Española</b>	1°22'30"S, 89°40'30"W	9	6048.0	1	45000	San Cristóbal	6	132.3
23	Islote Xarifa	1°21'24.5"S, 89°38'38.4"W	44	0.553	29	217	Española	9	133.4
14	Isla Gardner por Española	1°20'39.7"S, 89°38'49.8"W	44	58.038	29	966	Española	9	132.2
22	Islote Osborn	1°21'7.6"S, 89°38'55.3"W	44	1.698	29	430	Española	9	132.7
24	Islote Oeste	1°20'48.5"S, 89°39'42.2"W	44	0.376	29	83	Española	9	131.2
9	<b>Isla Santiago</b>	0°15'30"S, 90°43'30"W	37	58465.0	1	16860	Isabela	28	38.4
10	Isla Rabida	0°24'35"S, 90°42'30"W	28	499.312	28	4457	Santiago	28	25.2

Map Code <sup>1</sup>	Island Name <sup>2</sup>	Position	Pos. Ref. <sup>3</sup>	Area (ha)	Area Proximate Ref. <sup>3</sup>	Isolation (m)	Isolation From	Isol. Ref. <sup>3</sup>	Dist. to Center (km)
76	Roca Beagle Norte	0°24'40"S, 90°37'40"W	28	0.713	33	4805	Santiago	33	18.3
77	Roca Beagle Oeste	0°24'52"S, 90°37'53"W	28	4.262	33	5102	Santiago	33	18.3
78	Roca Beagle Sur	0°24'57"S, 90°37'46"W	28	8.730	33	5264	Santiago	33	18.1
40	Isla Sombrero Chino	0°22'2.5"S, 90°34'55"W	28	20.875	30	112	Santiago	30	20.0
52	Roca Bainbridge #1	0°20'27"S, 90°33'28"W	28	11.421	30	1024	Santiago	26	22.2
53	Roca Bainbridge #2	0°20'45"S, 90°33'22.5"W	28	2.896	30	1618	Santiago	30	21.6
41	Roca Bainbridge #3	0°20'55"S, 90°33'56"W	28	18.336	30	630	Santiago	30	21.5
54	Roca Bainbridge #4	0°21'24"S, 90°33'48"W	28	3.444	30	1228	Santiago	30	20.6
55	Roca Bainbridge #5	0°21'45"S, 90°33'56"W	28	4.072	30	1167	Santiago	30	20.0
56	Roca Bainbridge #6	0°21'56"S, 90°34'11"W	28	4.484	30	874	Santiago	30	19.8
57	Roca Bainbridge #7	0°22'23"S, 90°34'20"W	28	0.796	30	1350	Santiago	30	19.1
58	Roca Bainbridge #8	0°22'24"S, 90°34'37"W	28	0.647	30	1148	Santiago	30	19.2
46	Isla Bartolomé	0°16'51"S, 90°32'48"W	14	124.48	14	310	Santiago	14	28.6
79	Islote Gran Felipe	0°17'16"S, 90°33'5.5"W	14	0.039	14	567	Santiago	14	27.9
69	Islote Cousins	0°14'8.3"S, 90°34'29.1"W	44	0.858	27	2000	Santiago	27	34.0
92	Islote Logie	0°15'8"S, 90°34'37"W	27	0.200	36	100	Santiago	36	32.2
91	Islote Mao	0°9'15"S, 90°49'8"W	27	1.250	36	200	Santiago	36	53.9
43	Isla Albany	0°10'15"S, 90°50'44"W	27	12.733	5	669	Santiago	5	54.4
2	<b>Isla Marchena</b>	0°20'20"N, 90°28'25"W	38	12996.0	1	55800	Santiago	6	97.5
88	Islote Espejo	0°18'35"N, 90°24'16"W	38				Marchena		95.0
45	<b>Isla Genovesa</b>	0°19'40"N, 89°57'20"W	38	1410.8	1	46800	Marchena	6	114.8
1	<b>Isla Pinta</b>	0°35'18"N, 90°45'17"W	38	5940.0	1	28800	Marchena	6	127.7
47	<b>Isla Wolf</b>	1°22'30"N, 91°49'10"W	37	134.4	1	140400	Pinta	6	256.8
89	Islote La Ventana	1°21'45"N, 91°49'30"W	37	0.100	36	200	Wolf	36	256.0
L	Islote Norte de Wolf	1°23'30", 91°49'2"W	37	9.000	36	1000	Wolf	36	258.2
42	<b>Isla Darwin</b>	1°39'15"N, 92°0'20"W	37	106.3	1	175200	Pinta	6	296.0
E	Islote El Arco	1°39'30"N, 91°59'2"W	37	0.200	36	3000	Darwin	36	293.1
F	Islote El Torre	1°39'30"N, 92°0'40"W	37	0.100	36	200	Darwin	36	294.8

<sup>1</sup> The Map Codes are used in Figure One to indicate the relative locations of the islands.

<sup>2</sup> Our use of names are explained in the text. Several of the names used represent islands for which we could find no previous names. We encourage readers to tell us about other names for any of these islands. Islands are organized in this table in groups where large islands (in boldface) are followed by their satellite islands (indented). The list of satellites usually begin with a southern island and then progress eastward around the large island. Occasionally a satellite island will have its own set of satellite islands, these are arranged within the list.

<sup>3</sup> The various references are: 1 (Black 1973), 2 (Wiggins and Porter 1971), 3 (Snell et al. 1988), 4 (Cayot et al. 1994), 5 (aerial photo in CDRS library #692), 6 (Instituto Oceanografico de la Armada [IOA] 1980), 7 (IOA 1988b), 8 (IOA 1985), 9 (IOA 1991c), 10 (IOA 1990a), 11 (IOA 1990a, insert), 12 (IOA 1989b), 13 (IOA 1986b), 14 (IOA 1990b), 15 (IOA 1988c), 16 (IOA 1986a), 17 (IOA 1991d), 18 (IOA 1989a), 19 (IOA 1992b), 20 (IOA 1988a), 21 (Defense Mapping Agency Hydrographic / Topographic Center [DMA], 1984a), 22 (DMA 1984b), 23 (DMA 1983), 24 (DMA 1947a), 25 (DMA 1943b), 26 (DMA 1976a), 27 (DMA 1984c), 28 (DMA 1947b), 29 (DMA 1943a), 30 (aerial photo in CDRS library #47A), 31 (aerial photo in CDRS library #132), 32 (aerial photo in CDRS library #2104), 33 (aerial photo in CDRS library #225), 34 (aerial photo in CDRS library #288), 35 (aerial photos in CDRS library #'s 35 and 36), 36 (measured or estimated in the field by authors 1990 through 1994), 37 (IOA 1991a), 38 (DMA 1979), 39 (IOA 1991b), 40 (IOA 1993), 42 (British Admiralty 1987), 43 (IOA 1992a), 44 (Geographical Positioning System [GPS] readings taken by the authors 1990 - 1994).

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