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GUEST EDITORIAL

THE IMPACTS OF CLIMATE CHANGE ON THE GALAPAGOS ISLANDS: ASSESSING VULNERABILITY AND PLANNING FOR ADAPTATION

By: Giuseppe Di Carlo & Noémi d'Ozouville

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Historic data on thermal anomalies and El Niño events in the Eastern Tropical Pacific provide compelling evidence that Galapagos ecosystems have been exposed to rapid and abrupt oceanic and climatic changes in the past. However, their ability to adapt, if such changes become more frequent and persistent, is uncertain. This vulnerability to climate change is exacerbated by growing human pressures, driven by rapid economic growth, unregulated development, and immigration. These bring increasing numbers of cargo vessels, passenger boats and tourist flights, and invasive species. Over-fishing and rapid land-use change add to concern over loss of ecosystem integrity.

Given the uniqueness of the Galapagos environment, it becomes imperative to acquire a full understanding of this vulnerability and to find solutions to increase the resilience and adaptive capacity of the Galapagos. In this issue of *Galapagos Research* are several papers that developed from the "Climate Change Vulnerability Assessment of the Galapagos Islands", completed in 2009. This was a collaborative effort between Conservation International, the World Wildlife Fund, the Galapagos National Park and the Ecuadorian Ministry of the Environment, supported by the Charles Darwin Foundation and other Ecuadorian and international scientific institutions. On the 50th anniversary of the establishment of the Galapagos National Park and the Charles Darwin Foundation, the assessment was an initial study of how climate change may alter Galapagos ecosystems and how losses of ecosystem services may radically change its society. The articles on pages 26–61 of this issue provide evidence of past climate variability and ecosystem responses in the Galapagos through the analysis of recent fossil records at increasingly fine scales (Bush *et al.*), climate patterns and variability in the last 50 years (Wolff), and climate changes that the Galapagos should expect in the coming decades (Sachs & Ladd), including a review of the current Galapagos climate and the potential consequences of changing conditions on the dry and humid zones and

their native vegetation (Trueman & d'Ozouville). The potential effects of climate change on populations of two charismatic species, the Galapagos pinnipeds, are explored by Salazar & Denking.

The studies presented here, together with other unpublished studies that resulted from the assessment, provide evidence of the connectivity of the marine, coastal and terrestrial ecosystems and the great dependence of Galapagos society on their ecological services. This information allows managers, conservationists and scientists to understand the response of species and ecosystems to interactive effects of human activities, including climate change. But the outcomes of the assessment reach beyond the scientific evaluation of ecosystem responses, and work towards solutions for increasing the adaptive capacity of Galapagos ecosystems and the people that depend on them. Adapting to climate change is crucial to ensure the survival and continued well-being of ecosystems and human societies exposed to climate change. We believe that this initiative represents a real commitment, taken together by the people of the Galapagos, the Ecuadorian Government, NGOs and scientific institutions, towards increasing the capacity of marine and terrestrial ecosystems to maintain themselves and their services under future climatic conditions, for the benefit of society and the future generations of the Galapagos Islands.

The assessment was a collective effort between Conservation International, the Ecuadorian Ministry of the Environment, the Galapagos National Park and the World Wildlife Fund, supported by the Charles Darwin Foundation, the Centro Internacional para la Investigación del Fenómeno del Niño, the Universidad San Francisco de Quito and the University of North Carolina. We extend our most sincere gratitude to the authors who contributed to this issue and to all who participated in the assessment. Finally, we are grateful to the Charles Darwin Foundation and the Editor of *Galapagos Research* who encouraged the development of this special section.

RESEARCH ARTICLES

AN UPDATED CHECKLIST OF SCALE INSECTS (HEMIPTERA: COCCOIDEA) OF THE GALAPAGOS ISLANDS, ECUADOR

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SUMMARY

The information available on Coccoidea in the Galapagos Islands is sparse. Data on the species present, their distribution and host plants were compiled using recent information at the Charles Darwin Research Station and from the literature. Up to January 2008, 80 species from eight families were reported, more than doubling the total known in 2001. Of the 63 species whose origin has been determined, 50 are believed to have been introduced inadvertently on plants, fruits or vegetables, nine are endemic and four more are thought to be native. The low number of endemic and native species suggests that scale insects have been poor at reaching the islands naturally.

RESUMEN

Un inventario actualizado de los insectos escama (Hemiptera: Coccoidea) de las Islas Galápagos, Ecuador. La información disponible acerca de los Coccoidea de las Islas Galápagos es escasa. Datos de las especies presentes, su distribución y plantas hospederas fueron compiladas usando información de la Estación Científica Charles Darwin y la literatura. Hasta enero de 2008, 80 especies de ocho familias fueron reportadas, más que el doble del total conocido en 2001. De las 63 especies cuyo origen ha sido determinado, se cree que 50 han sido introducidas inadvertidamente sobre plantas, frutos o vegetales, nueve son endémicas y se piensa que cuatro son nativas. El bajo número de especies endémicas y nativas sugiere que los insectos escama no han sido buenos dispersándose a las islas en forma natural.

INTRODUCTION

Scale insects (Hemiptera: Coccoidea) are mainly small sap-sucking insects. They are widely distributed throughout the world except for the Arctic and Antarctic (Miller 2005). Many of the most successful species are pests of agriculture, horticulture and forestry (Miller & Davidson 1990, Miller *et al.* 2005), causing great economic losses annually (Kosztarab 1990). Individual species can infest leaves, fruit, branches, main stems, trunks or roots (Miller 2005). Because of their small size and habit of feeding in concealed areas, the insects are commonly transported on plant materials and frequently become invasive (Miller *et al.* 2005). Some species excrete large amounts of honeydew on which sooty moulds grow, which can cover the plant surface and severely restrict photosynthesis. Despite their small size, they are therefore economically and ecologically important on the Galapagos Islands.

Little is known about the Coccoidea of the Galapagos. The first specific surveys for them were carried out in 1973 and 1975 (Williams 1977), when few of the islands and habitats were examined. Prior to that, scale insects were occasionally found during general collections of invertebrates. The earliest records are of six species found on herbarium material collected by R. Snodgrass and E. Heller during 1898–9 and identified by Kuwana (1902) as *Orthezia galapagoensis* sp. nov., *Asterolecanium pustulans*, *Lecanium hemisphaericum*, *L. hesperidum pacificum* var. nov., *Aspidiotus lataniae* and *A. smilacis*. Morrison (1924) described five new species from material collected during the 1923 W. Beebe expedition: *Eriococcus papillosus*, *Margarodes similis*, *Phenacoccus parvus*, *Pseudococcus galapagoensis* and *P. insularis*. Two new species of mealybugs, *Rhizoecus insularis* and *Pseudococcus schusteri*, were described by Hambleton (1976) and Gimpel & Miller (1996) from specimens collected by R. Schuster in 1964. Williams (1977) reported three

undetermined diaspidids: *Chortinaspis* sp., *Velataspis* sp. and *Odonaspis* sp., the latter described by Ben-Dov (1988) as *O. galapagoensis* sp. nov.

Williams (1977) included 38 species from seven families in his review. An additional species, *Icerya purchasi*, was reported by Peck (2001), but he excluded an unidentified *Ceroplastes* species, thus leaving the total unchanged. Of these 38, nine are endemic to the Galapagos, two are native, 26 are thought to have been introduced inadvertently with imported plants, vegetables and fruits, and one is of undetermined origin.

Efforts to collect scale insects in the Galapagos intensified in 1998 when a project was initiated to evaluate the risks associated with using a ladybird predator (*Rodolia cardinalis*) to control the invasive scale insect, *Icerya purchasi* (Causton 2003, Causton *et al.* 2003). As part of this programme, it was necessary to identify which native scale insects could be at risk from the introduction of this predator. Plants, especially endemic species, were surveyed for scale insects and this provided many new scale insect species and host plant records. As a result of these surveys, it became obvious that there were many information gaps for this group and that other areas of the archipelago still needed to be surveyed. Since then, invertebrate monitoring by the Charles Darwin Research Station (CDRS), particularly recent surveys in agricultural and urban zones, has included the inspection of plants for scale insects.

Much of the information on scale insects in Galapagos is scattered in reports and databases. The objective of this study was to compile a comprehensive species list that included information on the distribution and host plants of scale insects present in the Galapagos Islands up until January 2008.

METHODS

Literature (including unpublished reports) and the invertebrates database of the CDRS were reviewed for records of scale insects. Specimens from the CDRS reference collection (IC CDRS) and specimens collected during recent surveys were identified by CH and DM.

In the following checklist, scale insect families are listed in alphabetical order, and new species, new islands and new host plant records since Peck (2001) are indicated with an asterisk. Following the species name and authority, status of the species is given in parentheses (E = endemic, found only in the Galapagos Archipelago; N = native, thought to occur naturally both in the Galapagos and elsewhere (usually Latin America); I = introduced, probably unintentionally brought to the islands in historical time by human agency or transport), then islands on which it occurs (Ba = Baltra; Bt = Bartolomé; Dp = Daphne; Dw = Darwin; Ed = Edén; Fe = Fernandina; Fl = Floreana; Ge = Genovesa; Is = Isabela; Ma = Marchena; PS = Plaza Sur; Pt = Pinta; Pz = Pinzón; Ra =

Rábida; SCl = San Cristóbal; SCz = Santa Cruz; SF = Santa Fé; SN = Seymour Norte; Sgo = Santiago) and finally host plants recorded.

RESULTS

Asterolecaniidae

Asterolecanium pustulans (Cockerell, 1892). (I) Is. *Tournefortia pubescens*.

A. puteanum Russell, 1935. (I) Is. *Croton scouleri* var. *scouleri*, *Waltheria ovata*.

Coccidae

Ceroplastes cirripediformis Comstock, 1881. (I) Ba, Bt, Ed?, PS, SCl*, SCz, Sgo. *Cryptocarpus pyriformis*, *Laguncularia racemosa*, *Maytenus octogona*, *Passiflora edulis**, *Rhizophora mangle*, *Tiquilia darwinii*, *Tournefortia* sp.

C. floridensis Comstock, 1881*. (I) SCl*, SCz*. *Citrus sinensis**, *Maytenus octogona**, *Zanthoxylum fagara**.

C. rusci Linnaeus, 1758*. (I) Is*, SCz*. *Annona muricata**, *Cordia lutea**, *Hibiscus rosa-sinensis**, *Laguncularia racemosa**, *Spondias purpurea**.

C. sinensis Del Guercio, 1900*. (I) SCz*, Sgo*. *Croton scouleri**, *Galvezia leucantha**, *Lycium minimum**.

Ceroplastes sp.* (?) Ed*, SCz*. *Annona cherimola**, *A. muricata**, *Cocos nucifera**, *Conocarpus erectus**, *Cordia lutea**, *Cyperus anderssonii**, *Galvezia leucantha**, *Mangifera indica**, *Maytenus octogona*, *Nerium oleander**, *Passiflora edulis**, *Pisonia floribunda**.

Coccus hesperidum Linnaeus, 1758. (I) Ba, Is, Pt, SCl*, SCz*, SN. *Cocos nucifera**, *Conyza bonariensis**, *Gossypium barbadense*, *Hibiscus rosa-sinensis**, *Ludwigia leptocarpa**, *Musa* sp., *Matisia cordata**, *Psidia carthagenensis**, *Psychotria rufipes*, *Roystonea regia**.

C. longulus Douglas, 1887*. (I) SCz*. *Citrus* sp.**, *Hibiscus rosa-sinensis**, *Rosa* hybrid cultivars*, *Terminalia catappa**.

C. viridis (Green, 1889). (I) Fl*, SCl*, SCz, Sgo*. *Cestrum auriculatum**, *Coffea* sp.**, *Inga* sp.**, *Laguncularia racemosa**, *Miconia robinsoniana**, *Musa* sp.**, *Psidium* sp., *P. guajava**.

Inglisia vitrea Cockerell, 1894*. (I) SCl*. *Annona cherimola**, *Inga* sp.*.

Parasaissetia nigra (Nietner, 1861). (I) PS, SCz. *Annona cherimola**, *Croton* sp., *Hibiscus* sp., *Maytenus octogona*.

Parasaissetia sp.* (?)*. SCz*. *Hibiscus rosa-sinensis**.

Pulvinaria psidii Maskell, 1893*. (I) SCl*, SCz*, SF*. *Chiococca alba**, *Citrus reticulata**, *Eriobotrya japonica**, *Miconia robinsoniana**, *Syzygium malaccense**.

P. urbicola Cockerell, 1893. (I) Fl*, SCz. *Annona muricata**, *Bryophyllum pinnatum**, *Tetramerium nervosum**.

Pulvinaria sp.* (?) Is*, SCl*, SCz*, SF*. *Blechum pyramidatum**, *Chiococca alba**, *Hibiscus rosa-sinensis**, *Hippomane mancinella**. *Maytenus octogona**.

Saissetia coffeae (Walker, 1852). (I) Fl*, Is, SCl, SCz. *Ageratum conyzoides**, *Annona cherimola**, *A. muricata**, *Bidens pilosa**, *Bryophyllum pinnatum**, *Calandrinia galapagosa**, *Cestrum auriculatum**, *Citrus* sp.**, *Chiococca alba*, *Cinchona pubescens**, *Coffea* sp.**, *Conyza bonariensis**, *Cordia lutea*, *Croton scouleri**, *Cyperus anderssonii**, *Epidendrum spicatum**, *Helianthus annuus**, *Hibiscus*

*rosa-sinensis**, *Justicia galapagana**, *Mangifera indica**, *Maytenus octogona**, *Melia azedarach**, *Pelargonium x hortorum**, *Piscidia carthagensis**, *Pseuderanthemum carruthersii**, *Psychotria rufipes*, *Rhizophora mangle*, *Ricinus communis*, *Ruellia malacosperma**, *Scalesia pedunculata*, *Sida rhombifolia**, *Syngonium sp.**, *Tetramerium nervosum**, *Thelypteris poiteana**.

S. miranda (Cockerell & Parrott, 1899). (I) SCL. *Sida sp.*

S. neglecta De Lotto, 1969. (I) Bt, PS. *Maytenus octogona*.

Saissetia sp.*. (I) SCz*. *Annona muricata**.

Conchaspidae*

Conchaspis angraeci Cockerell, 1893*. (I) SCL*, SCz*. *Begonia sp.**, *Cactaceae**, *Carica papaya**, *Croton scouleri**, *Epiphyllum oxypetalum**, *Hibiscus rosa-sinensis**, *Huernia aspera**.

Diaspididae

Aonidiella aurantii (Maskell, 1879)*. (I) SCL*, SCz*. *Cocos nucifera**, *Laguncularia racemosa**.

A. orientalis (Newstead, 1894)*. (I) SCL*, SCz*. *Allamanda cathartica**, *Annona cherimola**, *Citrus sp.**, *C. aurantium**, *Cocos nucifera**, *Melia azedarach**, *Nerium oleander**, *Terminalia catappa**.

Aspidiella hartii (Cockerell, 1895)*. (?) SCz*. *Miconia robinsoniana**.

Aspidiotus destructor Signoret, 1869. (I) SCz. *Parkinsonia aculeata**, *Phoenix dactylifera*, *Vallesia glabra*, *Zanthoxylum fagara**.

A. excisus Green, 1896*. (I) SCz*. *Castela galapageia**.

A. near pacificus Williams & Watson, 1990*. (I) SCz*. *Alternanthera halimifolia**, *Castela galapageia**, *Citrus sp.**, *Croton sp.**, *Phoenix dactylifera*, *Tournefortia rufo-sericea**, *Vallesia glabra*.

Chortinaspis sp.*. (E) SCz, SN. *Opuntia sp.*, *O. echios var. zacana*.

Chrysomphalus sp. (?) Sgo*. Host plants unknown.

Hemiberlesia lataniae (Signoret, 1869). (I) Ba, Is, Pt, SCL*, SCz, Sgo. *Acacia macracantha*, *Bursera graveolens*, *Cocos nucifera**, *Croton scouleri**, *Cryptocarpus pyriformis*, *Inga sp.**, *Scalesia incisa*, *Waltheria ovata*.

H. near rapax. (?) SCz*. *Miconia robinsoniana**.

Howardia biclavata (Comstock, 1883). (I) SCL, SCz, Sgo. *Acacia macracantha*, *Chiococca sp.**, *Citrus sinensis*, *Croton sp.**, *Waltheria ovata*.

Ischnaspis longirostris (Signoret, 1882)*. (I) SCz*. *Coffea sp.**, *Citrus sp.**.

Lepidosaphes beckii (Newman, 1867). (I) Fl*, SCz. *Citrus sp.*, *C. aurantium**, *Croton scouleri**, *Mangifera indica**, *Musa acuminata**.

Lepidosaphes sp.*. (?) SCz*. *Pseuderanthemum carruthersii**.

Melanaspis odontoglossi (Cockerell, 1893). (I) Is, SCz, Sgo. *Alternanthera filifolia*, *Conocarpus erectus*, *Croton scouleri var. scouleri*, *Cryptocarpus pyriformis*, *Maytenus octogona*, *Scalesia affinis*, *Waltheria ovata*.

Melanaspis tenebricosa (Comstock, 1881)*. (?) SCz*. *Zanthoxylum fagara**.

Odonaspis galapagoensis Ben-Dov, 1977*. (E) SCz*. *Sporobolus virginicus*.

Parlatoria crotonis (Douglas, 1887). (I) SCz. *Croton scouleri*.

Pinnaspis strachani (Cooley, 1899). (I) Bt, Fe, Fl*, Ge*, Is, PS, Pt, SCL*, SCz, Sgo, SN. *Abutilon depauperatum**, *Annona*

*muricata**, *Bastardia viscosa**, *Cassia occidentalis**, *Chamaesyce amplexicaulis*, *Chiococca alba**, *C. alba**, *Cocos nucifera**, *Conocarpus erectus*, *Cordia leucophlyctis**, *C. lutea*, *Croton scouleri*, *Citrus sp.**, *Cryptocarpus pyriformis*, *Cucumis dipsaceus**, *Euphorbia sp.*, *Gossypium sp.**, *G. barbadense*, *G. darwinii**, *Hibiscus rosa-sinensis**, *H. tiliaceus*, *Hippomane mancinella*, *Hyptis sp.**, *Lantana peduncularis**, *Mangifera indica**, *Neptunia plena*, *Nerium oleander**, *Parkinsonia aculeata*, *Passiflora quadrangularis**, *Polygala anderssonii*, *P. galapageia*, *P. sancti-georgii var. oblanceolata*, *Sansevieria trifasciata**, *Scalesia affinis*, *S. incisa*, *Scutia pauciflora*, *Sidapaniculata**, *Tiquilia darwinii*, *Tournefortia sp.*, *T. rufo-sericea**, *Vallesia glabra var. pubescens*, *Waltheria ovata*, *Zanthoxylum fagara**.

Pseudaulacaspis major (Cockerell, 1894). (I) SCz*, Sgo. *Annona muricata**, *Cordia lutea*, *Croton scouleri**, *Hippomane mancinella*, *Zanthoxylum fagara**.

Pseudoonidia trilobitiformis Green, 1896*. (I) SCz*. *Citrus limetta**.

Selenaspis articulatus (Morgan, 1889). (I) Fl*, Is*, SCL, SCz, Sgo. *Castela galapageia*, *Citrus sp.**, *C. limetta*, *Chiococca alba**, *Eriobotrya japonica**, *Hippomane mancinella**, *Inga sp.**, *Vallesia glabra var. pubescens*.

Unaspis citri (Comstock, 1883)*. (I) SCL*, SCz*. *Citrus sp.**, *Inga sp.**.

Velataspis sp. (E?) PS, Sgo. *Maytenus octogona*.

Eriococcidae

Eriococcus near dubius*. (?) SCz*. *Alternanthera halimifolia**, *Croton scouleri**.

E. papillosus Morrison, 1924. (E?) Bt, Is, SCz, Sgo, SN. *Alternanthera filifolia**, *Chamaesyce amplexicaulis*, *Croton scouleri*, *Cryptocarpus pyriformis*, *Euphorbia equisetiformis*, *Heliotropium angiospermum*, *Jasminocereus sp.*, *Tiquilia darwinii*, *T. nesiotica*, *Waltheria ovata*.

Eriococcus sp.*. (?) Is*. *Darwiniothamnus tenuifolius**.

Margarodidae

Icerya purchasi Maskell, 1878. (I) Ba, Ed*, Fe*, Fl, Ge*, Is, Ma, Pz, Pt*, Ra*, SCL, SCz, SF*, Sgo, SN. *Acacia insulae-iacobi*, *A. macracantha*, *A. nilotica**, *A. rorudiana*, *Acalypha abingdonii*, *Alternanthera echinocephala*, *Annona cherimola**, *Avicennia germinans**, *Bastardia viscosa*, *Bauhinia monandra*, *Begonia sp.**, *Blechum pyramidatum*, *Borreria ericaefolia*, *Brassica oleracea*, *Brickellia diffusa**, *Bursera graveolens**, *Cajanus cajan*, *Calandrinia galapagosa*, *Canavalia rosea*, *Centrolobium paraense*, *Chamaesyce amplexicaulis*, *C. viminea*, *Chiococca alba*, *Citrus sp.*, *C. aurantiifolia**, *C. sinensis**, *Clerodendrum molle**, *Cocos nucifera*, *Commicarpus tuberosus*, *Conocarpus erectus**, *Cordia leucophlyctis*, *Cordia lutea*, *Crotalaria incana**, *Croton scouleri*, *Cryptocarpus pyriformis*, *Cyclosporum leptophyllum*, *Cyperus anderssonii*, *Darwiniothamnus lancifolius*, *D. tenuifolius*, *Desmanthus virgatus**, *Desmodium glabrum**, *D. incanum*, *Euphorbia cyathophora**, *Ficus sp.**, *Gamochoeta purpurea*, *Gossypium darwinii*, *G. klotzschianum*, *Heliotropium angiospermum**, *Hibiscus rosa-sinensis**, *H. tiliaceus*, *Hyptis pectinata*, *Inga edulis**, *Ipomoea habeliana*, *I. nil*, *I. pes-caprae*, *Jasminocereus thouarsii**, *Laguncularia racemosa*, *Lantana camara**, *L. peduncularis*, *Lecocarpus*

darwinii, *L. pinnatifidus*, *Macraea loricifolia*, *Mangifera indica**, *Matisia cordata**, *Maytenus octogona*, *Merremia aegyptia*, *Mentha piperita*, *Nerium oleander*, *Neptunia plena**, *Ocimum basilicum*, *Parkinsonia aculeata*, *Passiflora quadrangularis**, *Phaseolus mollis*, *P. vulgaris*, *Phyllanthus carolinensis*, *P. acidus**, *Piscidia carthagenensis*, *Pisonia floribunda*, *Plumbago scandens*, *Polygala galapageia*, *Porophyllum ruderale**, *Portulaca oleracea**, *Prosopis juliflora*, *Psidium guajava**, *Psychotria rufipes*, *Punica granatum*, *Rhizophora mangle*, *Rhynchosia minima*, *Ricinus communis*, *Rosa* hybrid cultivars, *Russelia equisetiformis*, *Scaevola plumieri*, *Scalesia aspera*, *S. atractyloides*, *S. baurii*, *S. cordata*, *S. divisa*, *S. gordilloi*, *S. helleri*, *S. pedunculata*, *Scoparia dulcis**, *Senna obtusifolia*, *S. occidentalis*, *S. pistaciifolia*, *Stylosanthes sympodiales**, *Tectona grandis*, *Tournefortia psilostachya**, *T. rufo-sericea*, *Trema micrantha*, *Vallesia glabra*, *Vigna luteola**.

Margarodes similis Morrison, 1924. (E?) Ba, Bt*, Ed, SCz. *Bursera malacophylla*, *Maytenus octogona*, *Scaevola plumieri**.

Ortheziidae

Insignorthezia insignis (Browne, 1887). (I) Is*, SCL, SCz*. *Adenostemma platyphyllum**, *Ageratum conyzoides**, *Bidens riparia**, *Blechnum* sp., *Borreria laevis**, *Browallia americana**, *Dioclea* sp., *Diodia radula**, *Darwiniothamnus tenuifolius**, *Hyptis pectinata**, *Hypericum* sp., *Jaegeria gracilis*, *Justicia galapagana**, *Ludwigia leptocarpa**, *Mecardonia procumbens**, *Pseudelephantopus spicatus**, *Phyllanthus* sp., *Scalesia cordata*, *S. pedunculata*, *Scoparia dulcis**, *Stachytarpheta cayennensis**, *Tetramerium nervosum**, *Verbena litoralis*.

Praelongorthezia galapagoensis (Kuwana, 1902). (E?) Is, Pz, SCz*, Sgo, SN. *Bursera graveolens*, *Cordia lutea*, *Cryptocarpus pyriformis*, *Heliotropium angiospermum*, *Hibiscus rosa-sinensis**, *Scalesia microcephala*.

P. praelonga (Douglas, 1891). (I) Fe, SCL*, SCz*. *Capsicum* sp., *Chiococca alba** , *Citrus* sp., *Croton scouleri**, *Hibiscus* sp., *H. rosa-sinensis**, *Nerium oleander**, *Terminalia catappa**.

Praelongorthezia sp.*. (?) SCz*. *Pelargonium hortorum**.

Pseudococcidae

Antonina graminis (Maskell, 1897)*. (?) SCz*. *Digitaria horizontalis**, *Sporobolus virginicus**.

Chorizococcus nakaharai Williams & Granada de Willink, 1992*. (N?) Is*. Host plants unknown.

Chorizococcus sp.*. (?) SCz*. *Paspalum conjugatum**.

Dysmicoccus boninsis (Kuwana, 1909)*. (I) Fl*, SCL*, SCz*. *Citrus* sp.* , *Paspalum conjugatum**, *Saccharum officinarum**.

D. brevipes (Cockerell, 1893)*. (I) Fl*, Is*, SCz*. *Ananas comosus**, *Annona muricata**, *Cyperus anderssonii**.

Ferrisia virgata (Cockerell, 1893). (I) Ba, Is, SCz, Sgo. *Bursera graveolens*, *Tiquilia darwinii*, *Hibiscus tiliaceus*, *Hippomane mancinella*, *Ipomoea pes-caprae**, *Laguncularia racemosa*, *Tribulus cistoides*, *Waltheria ovata*.

Geococcus coffeae Green, 1933. (I) SCz. *Musa* sp.

Nipaeococcus nipae (Maskell, 1893)*. (I) Fl*, Is*, SCL*, SCz*. *Annona cherimola**, *A. muricata**, *Cocos nucifera**, *Psidium guajava**, *Hibiscus rosa-sinensis**.

Paracoccus solani Ezzat & McConnell, 1956*. (I) Ed*, Dp*, Is*, SCL*, SCz*, Sgo*. *Bougainvillea* sp.* , *Chamaesyce amplexicaulis** ,

*Galvezia leucantha**, *Gossypium* sp., *Hyptis* sp.* , *Heliotropium angiospermum**, *Lantana* sp.* , *Laguncularia racemosa**, *Scalesia aspera*, *Sida spinosa**, *S. hederifolia**, *Tribulus terrestris**.

Phenacoccus herreni Cox & Williams, 1981*. (I) SCz*. *Stictocardia tiliifolia**.

P. parvus Morrison, 1924. (I) Gen. Host plants unknown.

P. solenopsis Tinsley, 1898*. (I) SCL*, SCz*, Sgo*. *Annona muricata**, *Hibiscus* sp.* , *H. rosa-sinensis**, *Psidium guajava**, *Scalesia atractyloides**.

Phenacoccus sp.*. (N?) Fl*, SCz*. *Cordia* sp., *Lecocarpus pinnatifidus*.

Planococcus citri (Risso, 1813). (I) SCL, SCz. *Annona muricata**, *Alternanthera echinocephala**, *Asparagus officinalis**, *Blechnum pyramidatum*, *Cordia lutea**, *Croton scouleri**, *Cryptocarpus pyriformis**, *Huernia aspera**, *Ixora coccinea**, *Jatropha curcas*, *Miconia robinsoniana**, *Nerium oleander**, *Polyscias scutellaria**, *Psidium guajava*, *Ricinus communis*, *Scalesia pedunculata**, *Solanum cheesmaniae**, *Stictocardia tiliifolia**, *Tournefortia pubescens**.

P. minor? (Maskell, 1897)*. (I) Fl*, SCL*, SCz*. *Ananas comosus**, *Citrus reticulata**, *Hibiscus rosa-sinensis**, *Miconia robinsoniana**, *Phaseolus vulgaris**, *Psidium guajava**, *Sida paniculata**, *Solanum* sp.*.

Planococcus sp.*. (?) SCL*, SCz*. *Ananas comosus**, *Passiflora edulis**, *Solanum quitoense**.

Pseudococcus elisae Borchsenius, 1948*. (I) SCz*. *Tournefortia psilostachya**.

P. galapagoensis Morrison, 1924. (E) Ed, SCz. Host plants unknown.

P. insularis Morrison, 1924. (E) Ba. Host plants unknown.

P. near landoi (Balachowsky, 1959)*. (?) SCz*. *Ananas comosus**, *Passiflora* sp.* , *P. edulis**.

P. longispinus Targioni, 1867*. (I) SCz*. *Rosa* sp.* , *Nerium oleander**.

P. schusteri Gimpel & Miller, 1996*. (N?) SCz*. *Acacia macracantha**.

Pseudococcus sp. (?) Bt, Dw, Es*, Fe, Is, PS, Pz, SCz, Sgo, SN. *Alternanthera filifolia*, *Castela galapageia**, *Chamaesyce amplexicaulis*, *Cryptocarpus pyriformis**, *Jasminocereus* sp., *Laguncularia racemosa*, *Maytenus octogona*, *Opuntia* sp.* , *Scalesia affinis**, *S. incisa*, *S. villosa**, *Scutia spicata* var. *pauciflora*, *Vallesia glabra* var. *pubescens*, *Waltheria ovata**.

Rhizoecus insularis Hambleton, 1976. (E) SCz. *Hippomane mancinella*.

R. latus (Hambleton, 1946). (N) SCz. *Hippomane mancinella*.

Rhizoecus sp.*. (?) Is*. Host plants unknown.

DISCUSSION AND CONCLUSIONS

To date, 80 species from eight families have been reported from the Galapagos Islands. Of the 63 species whose origin has been determined, 50 are believed to be introduced species, nine endemic, and four are thought to be native.

The low numbers of endemic and native species suggest that scale insects have not been good at dispersing naturally to these islands, and most scale insect stages are indeed sedentary (Hodgson 2001). On the other hand,

many of the new records are of cosmopolitan pests that were probably introduced to Galapagos on imported fruits, vegetables or ornamental plants, particularly over the last decade, as population has increased rapidly and large amounts of such material have been brought in (CDF *et al.* 2008).

The number of new records (more than doubling the total in Peck 2001) suggests a need for more surveys to complete the checklist of scale insects of the Galapagos Islands.

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PROTHONOTARY WARBLER *PROTONOTARIA CITREA*, A NEW SPECIES FOR THE GALAPAGOS ISLANDS

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SUMMARY

We document the first record of Prothonotary Warbler *Protonotaria citrea* in Galapagos, on Española Island in 2007.

RESUMEN

La Reinita protonotaria *Protonotaria citrea*, una nueva especie para las islas Galápagos. Describimos el primer registro de la Reinita protonotaria *Protonotaria citrea* en Galápagos, Isla Española en 2007.

On 25 October 2007, GR, RP, W. Bustos, M. Oviedo, tourists and guides observed and photographed an unusual bird on Española Island (Fig. 1). At first it was thought to be an unusually coloured Yellow Warbler *Dendroica petechia*. However, GR later identified the bird as a male Prothonotary Warbler *Protonotaria citrea* on the basis of the strong and bright yellow color of the head and chest, and the contrastingly blue-grey wing and tail with extensive white flashes in the outer tail feathers. Subsequently, photographs of the bird permitted confirmation of the identification by P. Greenfield (pers. comm.). The bird seemed healthy, quite tame and was found foraging among the dry scrub vegetation at Punta Suárez.

This is the first record of a Prothonotary Warbler in Galapagos. The species is a migrant from North America, where it nests in an area from Minnesota to New York and from New Jersey to Texas and Florida (Meyer de Schauensee 1966). As a winter resident in Central and South America (including Ecuador) from September to April, it is found in secondary woodland and adjacent clearings and plantations, most often near water or lagoons (Ridgely & Greenfield 2001). It was first recorded in continental Ecuador (in Esmeraldas) in the early 20th century (Chapman 1926), with later records in San Lorenzo, Pichincha (Mindó) and Napo (Ridgely & Greenfield 2001).

With this report, the number of bird species recorded in Galapagos grows to 177, of which 56 breed in the islands (Wiedenfeld 2006, Jiménez-Uzcátegui *et al.* 2007).

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Figure 1. Prothonotary Warbler photographed on Española Island, 25 Oct 2007.

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MORPHOLOGICAL VARIATION OF GALAPAGOS ISLAND POPULATIONS OF THE YELLOW WARBLER *DENDROICA PETECHIA AUREOLA*

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SUMMARY

Culmen (beak) length and width, wing length and body mass varied significantly among six Galapagos island populations of the Yellow Warbler *Dendroica petechia aureola*. Culmen length and body mass were also significantly different between Galapagos and North American populations of *D. petechia*. Morphological differences among island populations of *D. p. aureola* may be related to resource variability and the presence of different bird species on different islands.

RESUMEN

Variación morfológica de las poblaciones del Canario María *Dendroica petechia aureola* de las islas de Galápagos. El largo y el ancho del pico, y la masa corporal, variaron significativamente entre las poblaciones del Canario María *Dendroica petechia aureola* de seis islas de Galápagos. El largo del pico y la masa corporal también fueron significativamente distintos entre las poblaciones de *D. petechia* de Galápagos y de Norte-América. Las diferencias morfológicas entre las poblaciones de *D. p. aureola* en las diferentes islas podrían relacionarse con la variabilidad de los recursos y la presencia de diferentes especies de aves en las diferentes islas.

INTRODUCTION

Studies of Galapagos birds have made significant contributions to our understanding of speciation and evolutionary processes, beginning with Darwin's observations and hypotheses to a series of modern investigations centered on finches Geospizinae (Grant 1999, Sato *et al.* 1999, Burns *et al.* 2002, Grant & Grant 2006). Key aspects of the Galapagos Islands as a model system to examine genetic divergence and genetic structure are their remoteness, fragmentation and age. The Galapagos Archipelago is *c.* 1100 km southwest of Central America, 1000 km from continental South America, and 720 km from Cocos Island (Costa Rica). Potassium-argon aging indicates a maximum age for currently emergent islands of less than six million years (Bailey 1976, Geist 1996), although a series of now submerged islands in this region may have formed more than 10 million years ago (Christie *et al.* 1992, Cox 1983, Geist 1996).

The Yellow Warbler *Dendroica petechia* occupies all major Galapagos Islands and many of the islets, where it is found in a variety of habitats but most commonly in littoral zone vegetation (Harris 1974). The diet is mainly arthropods, although fleshy fruit are also eaten (Castro & Phillips 2000, Guerrero-Gutiérrez 2002). Based on the rusty crown of mature males (Harris 1974, Castro & Phillips 2000), Yellow Warblers from the Galapagos Islands and Cocos Island have been recognized as a separate subspecies, *D. p. aureola* (Browning 1994, Lowther

et al. 1999). There appears to be little genetic structure in the Galapagos Yellow Warbler population, with a number of identical mtDNA haplotypes occurring on numerous islands dispersed throughout the archipelago (Browne *et al.* 2008). Although Yellow Warblers were previously thought to have colonized the Galapagos in historical times (Snow 1966, Steadman 1986) recent molecular evidence suggests that the Galapagos and mainland American populations diverged more than 37,000 years ago (Browne *et al.* 2008).

In this study, variation in culmen (beak) length, culmen width, wing length, and body mass are used to estimate morphological divergence among six Galapagos island populations. Divergence is also investigated between the *D. p. aureola* from the Galapagos Archipelago and *D. petechia* from three previously reported sites: Manitoba River delta (Canada), MacKenzie River delta, Alaska (U.S.A.) and northern South America (Lowther *et al.* 1999).

In addition, we present limited data on beak morphology for Galapagos populations of the Large-billed Flycatcher *Myiarchus magnirostris* and Grey Warbler Finch *Certhidia fusca*. The presence or absence of other competing species can result in morphological change in as short a period as a year, as demonstrated among species of Darwin's finches (Grant & Grant 2006). *M. magnirostris* and *C. fusca* are both potential competitors for food resources with *D. petechia* (Grant & Grant 1989, Tonnis *et al.* 2004). Although *D. petechia* are currently abundant on Floreana Island they are absent from the fossil record (Steadman

1986). It has been suggested that they are relatively recent arrivals to that island and may have thereby contributed to the apparent recent extinction of *C. fusca* from Floreana (Grant *et al.* 2005). However the two species coexist in the same habitat on other Galapagos islands (Lack 1947, Bowman 1961, Grant & Grant 2002).

METHODS

Adult *D. p. aureola* in the Galapagos were captured for morphological measurements in mist nets at the same locations on six islands where they were captured for a genetic study (Browne *et al.* 2008): Punta Cevallos (Española Island), 1°23.47'S, 89°37.15'W; Puerto Ayora (Santa Cruz), 0°40.12'S, 90°10.16'W; Post Office Bay (Floreana), 1°13.37'S, 90°27.37'W; Espumilla Beach (Santiago), 0°10.30'S, 90°30.32'W; Punta Pitt (San Cristóbal), 1°42.30'S, 89°14.90'W; Darwin Bay (Genovesa), 0°18.75'N, 89°56.45'W (study area 1 depicted in Fig. 3.1 of Grant & Grant 1989). All individuals were captured in May 2001 except those from Española which were captured in January 2001. On Santa Cruz, in addition to the ten individuals captured in 2001, eight additional adult birds from the highlands (Tortoise Reserve) were mist-netted in December 1981 by DJA. Morphological measurements were recorded only on adult males and females that could be confidently sexed. Morphological measurements consisted of culmen length measured from the anterior edge of the nostril to tip, culmen width measured at the anterior edge of the nostril, flattened wing chord (distance from bend of wrist to tip of ninth primary, with radius-ulna and manus held at right-angle), and body mass for all individuals with the exception of those sampled on Española, the first island visited, where only wing length and body mass were measured. Body mass was measured by weighing a bird in a mesh bag with a spring scale and the mass of the bag was recorded after the removal of the bird. Since DJA captured the individuals in 1981 and trained the other authors of this study, there was continuity in measurement techniques for the 1981 and 2001 collections. *M. magnirostris* and *C. fusca* that were captured incidentally in mist nets when sampling *D. p. aureola* were measured for culmen length, culmen width, wing length and mass. Morphological measurements are presented as means \pm SD.

RESULTS

Males and females in the combined Galapagos population (all individuals sampled, not weighted by island) were not significantly different in culmen length (males 9.36 ± 0.55 , $n = 19$; females 9.38 ± 0.32 , $n = 18$; $F_{1,35} = 0.05$, $P = 0.64$), culmen width (males 1.98 ± 0.18 , $n = 19$; females 2.11 ± 0.17 , $n = 18$; $F_{1,35} = 1.00$, $P = 0.33$) or mass (males 12.1 ± 1.06 , $n = 35$; females 11.9 ± 0.86 , $n = 26$; $F_{1,59} = 0.22$, $P = 0.33$), but were significantly different in wing length (males 64.07 ± 2.19 , $n = 35$; females 62.18 ± 2.14 , $n = 26$; $F_{1,59} = 11.06$, $P = 0.002$).

There were no significant differences in any of the measured variables between Santa Cruz *D. p. aureola* collected in 1981 and those collected in 2001.

Measurements of *D. p. aureola* (sexes combined) are presented in Table 1. Three of the four characters varied significantly among subpopulations (culmen length, $F_{4,32} = 7.9$, $P < 0.001$; culmen width, $F_{4,32} = 21.3$, $P < 0.001$; mass, $F_{5,56} = 9.5$, $P < 0.001$). Although wing length was not significantly different between islands for males and females combined ($F_{5,56} = 1.0$, $P = 0.44$), when separated by sex, wing length differed between islands for males ($F_{4,30} = 3.20$, $P = 0.027$) but not for females ($F_{3,22} = 3.20$, $P = 0.169$). Santa Cruz individuals had the shortest and narrowest beaks. Individuals from Española weighed the least, while individuals from Genovesa weighed the most and had the widest beaks.

There were no significant correlations among culmen length, culmen width, wing length and mass among island populations.

Comparable mean and variance measures for other *D. petechia* subspecies have only been reported for *D. p. amnicola* from Manitoba and *D. p. parkesi* from the MacKenzie River delta (Lowther *et al.* 1999). Combining all Galapagos populations, *D. p. aureola* were significantly larger than *D. p. amnicola* in male culmen length ($t_{76} = 11.9$, $P < 0.001$), female culmen length ($t_{38} = 19.4$, $P < 0.001$), male mass ($t_{194} = 11.9$, $P < 0.001$) and female mass ($t_{156} = 11.6$, $P < 0.001$), with no significant differences for male or female wing length. *D. p. aureola* were significantly larger than *D. p. parkesi* in culmen length (the only variable reported by Lowther *et al.* 1999) ($t_{53} = 16.3$, $P < 0.0001$). Additional culmen length means (without measurements of variance) have been reported for *D. p. rubiginosa* from Alaska and *D. p. banksi* from Yukon (Canada) (Browning 1994). The data from these

Table 1. Measurements (mean \pm SD) of *Dendroica petechia aureola* from six Galapagos Islands.

| | Culmen length (mm) | n | Culmen width (mm) | n | Mass (g) | n | Wing length (mm) | n |
|---------------|--------------------|----|-------------------|----|------------------|----|------------------|----|
| Genovesa | 9.23 \pm 0.51 | 4 | 2.27 \pm 0.12 | 4 | 13.45 \pm 1.04 | 4 | 63.00 \pm 3.19 | 4 |
| Santiago | 9.88 \pm 0.55 | 4 | 2.17 \pm 0.06 | 4 | 12.38 \pm 0.85 | 4 | 64.38 \pm 1.38 | 4 |
| Santa Cruz | 9.06 \pm 0.25 | 18 | 1.87 \pm 0.10 | 18 | 12.27 \pm 0.71 | 21 | 63.73 \pm 1.97 | 21 |
| San Cristóbal | 9.62 \pm 0.35 | 7 | 2.13 \pm 0.11 | 7 | 12.21 \pm 0.79 | 7 | 63.00 \pm 2.22 | 7 |
| Floreana | 9.72 \pm 0.23 | 4 | 2.14 \pm 0.01 | 4 | 13.15 \pm 1.30 | 4 | 63.20 \pm 1.96 | 4 |
| Española | | | | | 11.20 \pm 0.57 | 21 | 62.38 \pm 2.73 | 21 |

five sites indicate that culmen is 13–25 % longer in *D. p. auroela* than in *D. petechia* from northern Canada or Alaska.

No significant differences were found in culmen length, culmen width, mass and wing length between three island populations of *M. magnirostris* (Table 2). *M. magnirostris* are only vagrants to Genovesa (Castro & Phillips 2000, DJA pers. obs.) and no *M. magnirostris* were captured there or on San Cristóbal or Española. Culmen length and width of *C. fusca* for Genovesa ($n = 16$) were 7.51 ± 0.23 and 2.15 ± 0.13 , respectively; the mass was 9.43 ± 0.29 and wing length was 53.9 ± 1.41 . *C. fusca* were not captured on the other islands. These measurements indicate that *M. magnirostris* is 16 % heavier than Galapagos *D. p. auroela*, with a 12 % longer wing and a culmen that is 18 % longer and 29% wider. In contrast, *D. p. auroela* is 28 % heavier than *C. fusca*, with a 17 % longer wing and a culmen that is 25% longer but differs < 1 % in width.

DISCUSSION

Although no inter-island correlation occurred between any of the four measurements, statistical power was low since a maximum of six populations were measured. In a more extensive analysis of 617 skins of more than 40 breeding *D. petechia* populations from near the Arctic Circle to the equator, Wiedenfled (1991) found a significant negative correlation between body mass and latitude, with the largest individuals in the equatorial region, but reported only summarized statistics and did not include data from individual populations. Wing length, however, did not follow the overall size trend; although the longest wings occurred in the south, the shortest also occurred in the tropics (on Caribbean islands). Variation in wing length appears to be related to migratory distance. Although Wiedenfled (1991) did not give supporting data, he characterized Galapagos *D. p. auroela* as having a long tail and tarsus and proportionately short wing and bill. In general, body mass for *D. petechia* mass fluctuates seasonally and diurnally and in females is affected by presence of an egg in the oviduct (Baldwin & Kendeigh 1938, Wiedenfled 1991).

The pattern found in *D. p. auroela* of low levels of inter-island genetic variation (Browne *et al.* 2008), combined with significant differences in culmen length, culmen width and body mass on different islands, is also seen in Darwin's finches (Petren *et al.* 2005), land iguanas *Conolophus subcristatus* (Rassman 1997), giant tortoises

Geochelone spp. (Caccone *et al.* 1999, 2002) and *Opuntia* cacti (Browne *et al.* 2003, Helsen *et al.* 2009), all of which have distinct phenotypes among islands with shallow but significant levels of genetic divergence. In other organisms, including Galapagos mockingbirds *Nesomimus* spp. (Arbogast *et al.* 2006), land snails *Bulimulus* spp. (Parent & Crespi 2006) and darkling beetles *Stomion* spp. (Finston & Peck 2004) distinct morphological differences among islands are accompanied by more pronounced genetic differences.

The evolutionary origin of the observed differences in culmen length, culmen width and body mass for *D. p. auroela* on different islands might be due to chance (founder effects or genetic drift), possibly in combination with selection. Chance effects become less important with increasing movement of individuals among islands, accompanied by a decrease in genetic structure. The distribution of the same mtDNA haplotype on more than one island and the low level of genetic structuring among islands (Browne *et al.* 2008) suggest that effects other than chance influence beak morphology and body mass. Selection on trophic structures (bill dimensions) may result in character displacement, as shown for Darwin's finches (Grant 1999). The presence or absence of *M. magnirostris* or *C. fusca* could lead to character displacement in *D. p. auroela*, since all three species specialize on arthropods and eat at least small amounts of fruit (Grant & Grant 1989, Guerrero-Gutiérrez 2002). *M. magnirostris* is absent from some islands where *D. p. auroela* is present, such as Genovesa (Harris 1974, Castro & Phillips 2000). However, *C. fusca* is extremely common on Genovesa (Castro & Phillips 2000) and was the most common bird caught in our nets there (whereas in all other locations *D. p. auroela* was the most common bird caught). These differences in potential competitors may cause directional selection on trophic structures of *D. p. auroela*. On Genovesa, where the smaller *C. fusca* is common and the larger *M. magnirostris* is absent, displacement in some morphological traits of *D. p. auroela* toward a larger size might be predicted. This was not the case for wing length and culmen length (*D. p. auroela* on Genovesa had shorter culmens and wings than most other Galapagos subpopulations), but was found for culmen width and body mass (Genovesa birds had the highest values among all island subpopulations). A possible interpretation is that selection on Genovesa has favored "stouter" individuals, with more mass per unit of wing length and a thicker beak per unit of length, a morphotype that approximates that

Table 2. Measurements of *Myiarchus magnirostris* captured on Santa Cruz, Santiago and Floreana islands.

| | n | Culmen length (mm) | Culmen width (mm) | Wing length (mm) | Mass (g) |
|----------------|----|--------------------|-------------------|------------------|--------------|
| Santa Cruz | 11 | 10.93 ± 0.38 | 2.71 ± 0.14 | 70.23 ± 4.22 | 13.76 ± 0.71 |
| Santiago | 7 | 11.03 ± 0.41 | 2.72 ± 0.16 | 71.53 ± 4.69 | 13.92 ± 0.42 |
| Floreana | 3 | 11.14 ± 0.30 | 2.74 ± 0.11 | 72.09 ± 2.33 | 14.07 ± 0.39 |
| Above combined | 21 | 10.99 ± 0.37 | 2.72 ± 0.15 | 70.93 ± 4.74 | 13.86 ± 0.57 |

of the absent *M. magnirostris*, which deviates more from *D. p. aureola* in body mass than in wing length and more in culmen width than length.

The mtDNA data (Browne *et al.* 2008) indicate significant genetic divergence between Galapagos *D. petechia* and populations from the American continents. The rusty crown of Galapagos *D. p. aureola* clearly separates it from other *D. petechia* populations. Our results show that Galapagos *D. p. aureola* are also significantly larger than at least some North American populations in culmen length, culmen width and body mass. Passerines on islands usually have larger bodies and bills than mainland populations of the same species (Grant 1965, Lack 1971, Clegg & Owens 2002). A larger bill may permit use of a wider range of resources, and an increase in body size may reflect a more “generalist” strategy (Scott *et al.* 2003). However, Galapagos *D. p. aureola* appear to have similar mass and bill size to those from the Pacific coast of South America (Wiedenfeld 1991).

Our study was based on small samples from each island and should be considered preliminary. Additional studies will be necessary before robust conclusions can be made about inter-island variation of *D. p. aureola* or differences between Galapagos birds and continental populations of *D. petechia*.

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FIRST INVENTORY OF ANTS (HYMENOPTERA: FORMICIDAE) ON BALTRA ISLAND, GALAPAGOS

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SUMMARY

Baltra island is vulnerable to ant invasions because it is one of the principal ports of entry to the Galapagos archipelago. In spite of this, little was known about its ant fauna. We present 13 new records of ants for Baltra collected during 2005 and 2006: *Tapinoma melanocephalum*, *Camponotus planus*, *Paratrechina longicornis*, *Paratrechina* sp., *Monomorium destructor*, *M. floricola*, *Pheidole* sp., *Solenopsis geminata*, *S. globularia pacifica*, *Tetramorium bicarinatum*, *T. lanuginosum* and *T. simillimum*. In addition to this, we report a new species for Galapagos: *Monomorium* sp. nr. *pharaonis*. *S. geminata* and *M. destructor* are considered threats to native fauna

RESUMEN

Primer inventario de las hormigas (Hymenoptera: Formicidae) en la Isla Baltra, Galápagos. La isla de Baltra es uno de los puntos vulnerables a la introducción de hormigas invasivas ya que es uno de los puertos principales del archipiélago de Galápagos. Pese a ello durante mucho tiempo la isla ha permanecido poco conocida en cuanto a su myrmecofauna. Presentamos 13 registros nuevos de hormigas para Baltra colectados durante 2005 y 2006; *Tapinoma melanocephalum*, *Camponotus planus*, *Paratrechina longicornis*, *Paratrechina* sp., *Monomorium destructor*, *M. floricola*, *Pheidole* sp., *Solenopsis geminata*, *S. globularia pacifica*, *Tetramorium bicarinatum*, *T. lanuginosum* and *T. simillimum*. Incluimos al resultado un nuevo registro de hormiga para Galápagos: *Monomorium* sp. c. *pharaonis*. Identificamos a *S. geminata* y *M. destructor* como las especies de mayor amenaza a la fauna nativa.

INTRODUCTION

Baltra is a small island (25.1 km²) that lies north of the island of Santa Cruz. The vegetation is similar to that of northern Santa Cruz and is dominated by native and endemic plants such as *Bursera malacophylla* B.L. Rob, *Chamaesyce punctulata* (Andersson) D.G. Burch, *Cordia lutea* Lam., *Crotalaria pumila* Ortega, *Opuntia echios* var. *echios*

Howell, *Panicum alatum* var. *minus* (Andersson) Zuloaga & Morrone, *Parkinsonia aculeata* L., and *Scalesia crockeri* Howell, and with important introduced elements such as *Cleome viscosa* L. (Wiggins & Porter 1971). Baltra has also been altered by human activities including the introduction of exotic animals. During the Second World War, Baltra was converted into a U.S. military base and in 1946 was placed under the jurisdiction of the armed forces of

Ecuador (Hamann 1979, 1981). Currently, Baltra airport is the main airport of entry for visitors and imported goods from mainland Ecuador and consequently it is considered as a major entry point for alien species including ants (Meier 1994).

Although ants are considered some of the most invasive organisms worldwide (McGlynn 1999), little attention has been paid to this group in the Galapagos and an inventory has not been carried out on Baltra. Prior to this study, only three species had been collected on Baltra: *Camponotus zonatus* Emery, an introduced ant (formerly *C. conspicuus zonatus*: W. Mackay pers. comm.); *Cylindromyrmex whymperi* (Cameron), a species of undetermined native/introduced status (previously identified for Galapagos as *C. striatus* Mayr: Andrade 1998) and *Dorymyrmex pyramicus albemarlensis* Wheeler, possibly endemic (F. Cuezco pers. comm.). The objective of this study was to carry out the first complete inventory of ants on Baltra in order to determine the composition of its ant fauna and identify species that may be potential threats for the archipelago.

MATERIALS AND METHODS

Two surveys were conducted. The first was carried out from 14 to 16 August 2005, when collecting locations included human settlements, the airport, rubbish dump, dock at Itabaca Canal, some less disturbed natural areas, and the site of repatriation to Baltra of the Land Iguana *Conolophus subcristatus* Gray (Fig. 1). Eleven sites were sampled in total. All locations were georeferenced using hand held Global Positioning System units (GPS). A second survey, 19–20 April 2006, was conducted at the Land Iguana colony because this was an area where *C. whymperi* and *D. pyramicus albemarlensis* had been recorded previously and these species were not recorded during the first collecting survey. At each location, one 4 x 1 cm tube containing either a honey or a tuna bait was placed alternately every 10 m along a transect approximately 200 m long (Fig. 1). On the first survey a total of 630 baits was placed along 30 transects and on the second survey 168 baits were placed along eight transects. Baits were placed from 6h00 to 8h00 and from 17h00 to 20h00. The

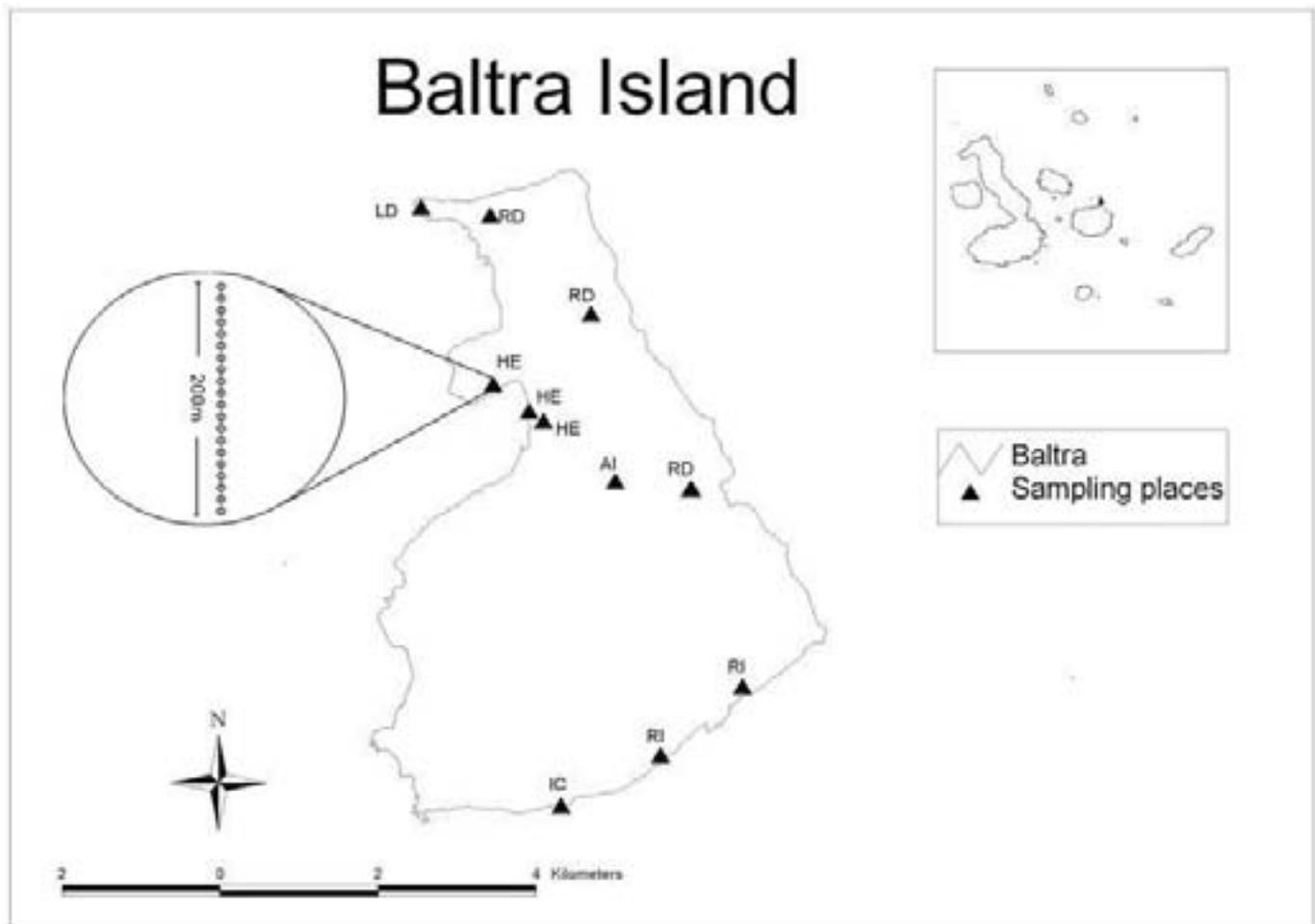


Figure 1. Sampling locations: AI = airport; HE = human settlements; IC = dock at Itabaca Canal; LD = less disturbed areas; RD = rubbish dumps; RI = site of repatriation of Land Iguanas. Enlarged circle shows the layout of baits on the transects, although the orientation of each transect differed.

rubbish dump and the housing of the Ecuadorian Airforce were also surveyed, at 12h00–14h00. Additional specimens were collected by Galapagos National Park guards using peanut butter baits in October and November 2006.

At each collecting site, tree trunks, leaf litter and soil were checked manually for ants. Specimens were taken to the Charles Darwin Research Station (CDRS) where they were processed and identified. Specimens from Baltra housed in the CDRS museum were also identified. All specimens were deposited in the Invertebrates Reference Collection at CDRS (IC CDRS). Specimens of *Monomorium* sp. nr. *pharaonis* were also deposited at The Natural History Museum, London (BMNH). Digital pictures of all species may be found at <<http://www.antweb.org/galapagos.jsp>>.

RESULTS AND DISCUSSION

As a result of these surveys an additional 13 species were registered on Baltra bringing the total known from that island to 16: 10 introduced, one endemic, one possibly endemic and four species of unknown status. Nine of the species belong to the subfamily Myrmicinae, followed by Formicinae (4), Dolichoderinae (2) and Cerapachyinae (1). Eight species are “tramp ants”, species that have been dispersed worldwide through trade (Table 1).

We did not find two of the three ant species reported previously from Baltra: *C. whymperi* and *D. pyramicus albemarlensis*. *C. whymperi* (two workers and a female) was

collected during the Harrison Williams expedition at the southern end of the island (Wheeler 1924) and also by C. Marquez in 1991 on *Maytenus octogona* (L’Hér.) DC. next to Caleta de las Tintoreras (C. Marquez pers. comm.). It is reported from Baltra, Fernandina, Isabela and Santa Cruz (Wheeler 1924, Silberglied 1972, Clark et al. 1982). *D. pyramicus albemarlensis*, was collected by L. Roque-Albelo in 1991 (exact location not recorded) and at the airport by S. Abedrabbo in 1992. This species is reported from Eden, Española, Fernandina, Genovesa, Isabela, Marchena, Pinta, Santa Cruz, Santa Fe (IC CDRS database). It is possible that aggressive ants such as *Solenopsis geminata* (Fabricius) and *Monomorium destructor* (Jerdon) have influenced the distribution of these two species of ant.

Camponotus planus Smith was the only endemic species to be collected during the surveys. It is nocturnal and is typically found on the coast of this island. On Baltra we observed it to displace the introduced carpenter ant, *C. zonatus*, at baits. In areas occupied by *S. geminata* or *M. destructor*, *C. planus* was displaced at baits.

On Baltra, *C. zonatus*, *M. destructor*, *Monomorium* sp. nr. *pharaonis*, *Paratrechina longicornis* (Latreille), and an unidentified *Paratrechina* species are widely distributed and apparently have established colonies throughout most of the island. *Solenopsis globularia pacifica* Wheeler, an unidentified *Pheidole* species and the tramp species *Monomorium floricola* (Jerdon), *S. geminata*, *Tapinoma melanocephalum* (Fabricius), *Tetramorium simillimum* (Smith), *Tetramorium bicarinatum* (Nylander), and *Tetramorium lanuginosum* Mayr

Table 1. Ant records for Baltra. (x) = species collected previously but not reported in this study; x = species present; new species for Baltra in bold; * new record for Galapagos.

| SUBFAMILY <i>Species</i> | Sites ¹ | | | | | | | | Tramp/ Invasive? | First record in Baltra | Status ² |
|--|--------------------|----|----|----|----|----|----|-----|---------------------|------------------------|---------------------|
| | AI | HE | IC | LD | RD | RI | LU | | | | |
| CERAPACHYINAE | | | | | | | | | | | |
| <i>Cylindromyrmex whymperi</i> | | | | | | | | (x) | - | 1924 | ? |
| DOLICHODERINAE | | | | | | | | | | | |
| <i>Dorymyrmex pyramicus albemarlensis</i> | (x) | | | | | | | (x) | - | 1992 | E? |
| <i>Tapinoma melanocephalum</i> | x | x | x | | | | | | T | 2005 | I |
| FORMICINAE | | | | | | | | | | | |
| <i>Camponotus planus</i> | | | | x | x | | | | x | 2005 | E |
| <i>Camponotus zonatus</i> | x | x | x | x | x | x | | | - | 1992 | I |
| <i>Paratrechina longicornis</i> | x | x | x | x | x | x | | | T | 2005 | I |
| <i>Paratrechina</i> sp. | | x | x | x | | | | | - | 2005 | ? |
| MYRMICINAE | | | | | | | | | | | |
| <i>Monomorium destructor</i> | x | x | | x | x | x | | | T | 2005 | I |
| <i>Monomorium floricola</i> | | | | x | | | | | T | 2005 | I |
| * <i>Monomorium</i> sp. nr. <i>pharaonis</i> | x | x | x | | x | x | | | - | 2005 | I |
| <i>Pheidole</i> sp. | | | | | | x | | | - | 2005 | ? |
| <i>Solenopsis geminata</i> | | x | | | | x | | | T/I | 2005 | I |
| <i>Solenopsis globularia pacifica</i> | | x | x | | | | | | - | 2005 | ? |
| <i>Tetramorium bicarinatum</i> | x | | | | | | | | T | 2005 | I |
| <i>Tetramorium lanuginosum</i> | | x | x | x | | | | | T | 2005 | I |
| <i>Tetramorium simillimum</i> | | x | | | | | | | T | 2005 | I |

¹Site codes as in Fig. 1; LU = Location undetermined.

²E = Endemic; E? = Possibly endemic; I = Introduced; ? = Undetermined.

are not widely distributed on Baltra, and are found principally in the human settlements.

Most of the species found on Baltra are distributed widely in the archipelago with the exception of *M. destructor* and *T. lanuginosum*. These two species have previously been reported from Puerto Velasco Ibarra on Floreana Island (Pezzatti *et al.* 1998, Aesch & Cherix 2005). Recently, *M. destructor* has also been registered on Isabela and Santiago islands (H.W.H. unpubl. data).

The introduced species *T. melanocephalum*, *P. longicornis*, *M. floricola* and *T. lanuginosum* are considered lesser threats to Galapagos fauna (Causton *et al.* 2006). *T. bicarinatum* was suggested as the possible causal factor of the displacement of *Camponotus macilentus* Wheeler during the El Niño event of 1982 on Española Island (Lubin 1985), but has not been observed to be invasive (in the sense of causing ecological damage). Little is known about the impact of *C. zonatus* in Galapagos or other parts of the world and studies are needed to determine its potential to become invasive in the archipelago.

The fire ant *S. geminata* is considered invasive in Galapagos and there is concern that *M. destructor*, first recorded in Galapagos in 1997, is also becoming invasive (Causton *et al.* 2006). *M. destructor* and *S. geminata* have been shown to be highly dominant and competitive at baits on Floreana Island (Aesch & Cherix 2005). On Baltra, both species displaced the introduced *C. zonatus*, undetermined beetles and cockroaches from honey baits. Displacement at baits of other ant species by *S. geminata* and *M. destructor* was not observed on Baltra. However, in the area of repatriation of iguanas, both species quickly monopolized the baits and the baits were not approached by other invertebrates. *S. geminata* has been identified as a threat to other invertebrates as well as to young and weak Land Iguanas (Williams & Whelan 1991, Roque-Albelo & Causton 1999). High numbers of *M. destructor* were found at most collecting sites on Baltra, in both natural and

inhabited areas, whereas on Floreana it is restricted to the port area (Pezzatti *et al.* 1998, Aesch & Cherix 2005). The impact of *M. destructor* in Galapagos has not been studied, although it is widely regarded as a threat to biodiversity in the Pacific. It also chews on telephone cabling and electrical wires, and could therefore affect the operation of the airport on Baltra. The control of *M. destructor* and *S. geminata* on Baltra and in other parts of the archipelago is currently a priority for the Galapagos National Park Service.

On Baltra, *P. longicornis*, *Monomorium* sp. nr. *pharaonis* and *M. destructor* were observed tending the invasive scale insect *Icerya purchasi* Maskell and aphids on *Catharanthus roseus* (L.) G. Don, *Sida ciliaris* L. and an *Acacia* sp. These ants may aid in the transportation, and hence dispersal, of homopterans as well as help build up their population numbers.

One new record for Galapagos is from the subfamily Myrmicinae: *Monomorium* sp. nr. *pharaonis* (Fig. 2). It was attracted to tuna bait at the dock at Itabaca Canal (0°28'59.52" S, 90°16'39.84" W), in the littoral zone at 5–15 m altitude, 16 Oct 2005; 20 workers were collected (H. Herrera & R. Azuero, HWH 154, at IC CDRS and BMNH). This taxon has so far been recorded only in California and India (P.S Ward & B. Heterick pers. comm.), but a review of specimens at IC CDRS revealed that it has also been previously collected on Santa Cruz and San Cristobal in the Galapagos islands. It possibly originates from India or southeast Asia and its precise identification awaits a full revision of the Oriental *Monomorium* species (B. Bolton pers. comm.). The date of its establishment in Galapagos and its impact on Galapagos ecosystems are unknown.

CONCLUSIONS AND RECOMMENDATIONS

Many of the ant species found on Baltra are tramp ants introduced by humans. These are still mainly restricted to human settlements and the Itabaca Canal dock, which



Figure 2. *Monomorium* sp. nr. *pharaonis* worker, face and lateral views.

is used for movement of passengers and goods to and from Santa Cruz Island. *Monomorium* sp. nr. *pharahonis*, *T. lanuginosum* and *M. destructor*, the last two previously found only on Floreana, may be more widely distributed in the archipelago than current records indicate.

S. geminata and *M. destructor* are considered serious threats to Baltra island's biodiversity and we recommend that the area occupied by these species be defined and a management plan developed as soon as possible. Because Baltra is a principal port of entry for invasive ants we suggest intensifying current monitoring protocols so that surveys are conducted monthly. This will help ensure the early detection of newly introduced species that are a serious threat to Galapagos, such as the Argentine Ant *Linepithema humile* (Mayr), the Red Imported Fire Ant *Solenopsis invicta* (Buren) and the Big-headed Ant *Pheidole megacephala* (Fabricius).

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A PILOT SURVEY OF THE CENTRAL COLONY OF THE WAVED ALBATROSS *PHOEBASTRIA IRRORATA* ON ESPAÑOLA ISLAND

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SUMMARY

Española Island is the main breeding site of the Waved Albatross *Phoebastria irrorata* but little is known of the nesting populations other than those at Punta Cevallos and Punta Suárez. In May 2008 we located nesting albatrosses from nearly the top of the island to the south coast (the “Central Colony”), including in areas not previously reported. We found evidence of a strong interaction between the distribution of woody vegetation and nesting albatrosses. Many albatrosses nest in areas too overgrown to fly into, and walk long distances to and from more open take-off and landing points. Tortoises facilitate albatross movement and nesting by creating trails that albatrosses use. The need remains for a comprehensive estimate of albatross population size and distribution that includes both coastal and inland populations.

RESUMEN

Un reconocimiento piloto de la Colonia Central del Albatros de Galápagos *Phoebastria irrorata* en la Isla Española. La Isla Española es el principal sitio de anidación del Albatros de Galápagos *Phoebastria irrorata* pero poco se conoce sobre las poblaciones anidantes excepto por aquellas de Punta Cevallos y Punta Suárez. En mayo 2008 encontramos albatroses anidando desde cerca de la cumbre de la isla hasta la costa sur (la “Colonia Central”), incluyendo áreas no reportadas previamente. Encontramos evidencia de fuerte interacción entre la distribución de vegetación leñosa y los albatroses anidantes. Muchos albatroses anidan en áreas demasiado enmarañadas para entrar volando, y caminan largas distancias desde y hacia zonas de aterrizaje y despegue más despejadas. Las tortugas facilitan el movimiento y anidación de los albatroses al crear senderos que los albatroses usan. Aún falta un completo estimado del tamaño de población y distribución del albatros que incluya las poblaciones costeras e interiores.

INTRODUCTION

The Waved Albatross *Phoebastria irrorata* is designated as Critically Endangered, with an apparently declining population (Anderson *et al.* 2008). It is the only species of albatross that breeds in the equatorial zone and its distribution, both for breeding and foraging, is extremely limited (Tickell 1996). Its foraging range extends from the Galapagos Islands to the section of the South American coast from the equator south to northern Peru (Anderson *et al.* 2003). Waved Albatrosses are philopatric breeders and nest almost exclusively on Española Island, the south-easternmost island in the Galapagos Archipelago. Some 10–20 breeding pairs have also been recorded on Isla de la Plata off the coast of Ecuador, but long-term data on these birds are scarce. Additionally, a small number of non-breeding birds occasionally inhabit Genovesa Island, Galapagos (Anderson *et al.* 2002).

The status and trend of the nesting population remain uncertain despite attempts to characterize them island-wide (Harris 1973, Douglas 1998, Anderson *et al.* 2002, Awkerman *et al.* 2006). In particular the status of the “Central Colony” of Douglas (1998) has long been uncertain

(Anderson *et al.* 2002, 2008). This and other colonies were surveyed in 1970 and 1971 by Harris (1973) and in 1993–4 by Douglas (1998), but incomplete coverage and non-standardized census methods generate uncertainty about the resulting population estimates. The current status of the Central Colony is of particular interest because of the large area that it may occupy and hence the nesting population that it may support. Additionally, it has been postulated that declines in albatross nesting populations could be associated with widespread re-generation of woody vegetation on the island since eradication of feral goats *Capra hircus* in 1978 (Anderson *et al.* 2002, 2008). If this is the case, the Central Colony would be most susceptible to such changes as woody plant regeneration has been more prolific in the interior of the island than at its eastern and western points (Punta Cevallos and Punta Suárez), which host the best-known albatross populations.

METHODS

Difficulty of access due to dramatic growth of woody vegetation has constrained surveying the Central Colony. We reached the higher regions of the island along trails

established to monitor the tortoise population. These end at the “El Caco” tortoise nesting area (Fig. 1), and from there we walked to areas where we predicted we might find nesting albatrosses based on Harris’s (1973) map of former distributions. All fieldwork reported here was conducted between 22 and 31 May 2008.

RESULTS AND DISCUSSION

We found nesting albatrosses from nearly the top of the island to the south coast (Fig. 1). Due to time constraints, we were not able to determine how far the colony extended to the east and west of the areas searched, but encountered no obvious decline in densities of birds as we moved east and west. Therefore, we suspect that the Central Colony occupies a far greater area than we were able to search. Additionally, satellite imagery (0.6 m resolution Quick-Bird) indicated a number of areas with little woody vegetation cover elsewhere on the southern slope of the island, similar to areas in which we observed nesting albatrosses. We found substantial numbers of nesting birds in areas not reported by Harris (1973) or Douglas (1998). Moreover, from a viewpoint on a large rock protruding above the woody canopy, we observed albatrosses landing in inland areas far to the west and east of where Harris (1973) and Douglas (1998) had mapped them. Thus, the nesting distribution of albatross has either changed considerably or was never adequately documented.

During a one-day transect survey devoted solely to estimating abundance, we encountered 274 albatrosses in 188 clusters (single or multiple birds within 1 m of one another, maximum cluster size = 7 birds) for an encounter rate of 30 clusters per hour. The average encounter rate was a single bird or cluster of birds every 20 m. During this survey, qualitative observations indicated an



Figure 1. Route of access to Central Zone and locations of albatross (open dots) and tortoises (filled dots) encountered on 24 May 2008 and subsequent days.

interaction between the distribution of albatrosses and woody vegetation. First, within the Central Colony there are large areas of dense vegetation that lack nesting albatrosses. Few comparably sized open areas lacked albatrosses; those that did tended to be in the lee of promontories and with little wind, and hence likely difficult for albatrosses to fly into. Nesting birds were scattered throughout available habitat, some in full sun and others in shade, but generally all within 100 m of prominent take-off points which the albatross walked to along well-beaten paths. Take-off points were generally on exposed slopes with a track 50–100 m long and 20–50 m wide, oriented into the prevailing southeasterly winds. We termed these areas “airports” because albatrosses converged on them, grouped together at the upwind end, and took turns in attempting to take off on wind gusts (Fig. 2). We suspect that the feet of the albatrosses, which initiate flights by running, maintain the low, sparse vegetation on these “airports”. A network of grassy tracks led away from each airport and seemed also to be maintained in this way.

That birds aggregated in large numbers to take off from few sites, and that they traveled significant distances to reach them, suggests that airports are limiting. We watched one airport for c. 30 min., when eight of 12 take-off attempts were aborted. Generally birds aborting flights crash-landed safely on the grassy substrate, but in some cases their wings struck woody vegetation. Dead fallen and hardened woody limbs and stems extending up from ground level seemed to present as much or more of a hazard than did the branches of living trees. Although we found some dead albatrosses, we did not observe any obviously associated with flight hazards.

We do not know why albatrosses nest in the central zone, which is distinct from coastal areas in climate, vegetation and accessibility. Waved Albatrosses are long-lived and highly philopatric; the Central Colony may comprise descendants of individuals (or even in some



Figure 2. Waved Albatross “airport” in the Central Colony, with bird “testing” incipient gust for potential to support take-off (photo: Hara Woltz).

cases the individuals themselves) that occupied the area when it was maintained in a more open state first by tortoises and then by goats. There may also be other advantages of nesting in the Central Zone. We hypothesize a lower incidence of mosquitoes and possibly ticks, flies and other pests of nesting albatross (Awkerman *et al.* 2005), as well as fewer other seabird hosts to support populations of these ectoparasites, in the island's interior.

We observed a fairly broad zone of overlap between tortoises and albatrosses, and twice observed them interacting. One large male tortoise was seen moving rapidly through the colony, evoking little response by the birds that he passed. On another occasion, a female tortoise walked toward a group of nesting albatrosses but veered away once they rose from their nests (Fig. 3). Also, in the area where tortoises overlapped with albatrosses the vegetation was noticeably easier to move through. We observed albatrosses walking to airports via swaths of grass flattened by tortoises, whereas where tortoises did not occur albatrosses used narrower and more sinuous albatross-made trails. In the portion of the Central Colony occupied by a large number of tortoises we encountered several abandoned albatross eggs but none of them broken; it therefore seems unlikely that tortoises commonly crush albatross eggs at present densities. Further study of tortoise-albatross interactions would be useful, but we surmise that they are largely neutral to positive, with tortoises facilitating albatross movement and nesting by creating more open trails and by pulling down low vines and shrubs that would obstruct movement by albatrosses. Nevertheless, we believe that the positive effects of tortoises on albatrosses in the Central Colony will increase only slowly as tortoises spread onto the southern slopes from their repatriation zones on the island's north side. The reason is that there are few *Opuntia* cacti (a key source of food, water and shade for much of the year) present in the Central Colony area to attract the tortoises, and the rate of spread of *Opuntia* from the small groups remaining after goat depredation is also slow.

An experimental vegetation manipulation, if deemed worthwhile by the Galapagos National Park, could generate insights on the potential for woody vegetation to limit nesting activities by the albatross on Española and determine whether vegetation management might be warranted until the tortoise population becomes fully re-established. We estimate that the effort required to remove woody vegetation (branches of living plants as well as dead wood) from experimental plots would be minimal insofar as a total area of < 1 ha across multiple plots could be sufficient to generate reliable inference, once the baseline of nesting densities on plots is established. Any such experiment should assess community-wide responses, not just the effect on nesting albatrosses.

We conclude that the Central Colony hosts many nesting albatrosses and warrants more thorough survey, to determine the potentially large fraction of the species' population that might nest in inland areas. Given the



Figure 3. Co-occurrence of giant tortoises and nesting Waved Albatrosses in the Central Colony (photo: Hara Woltz).

dense brush over much of the island, the best prospect for a complete survey might be high resolution day-time video or still photography or night-time infrared photography during the incubation period, from fixed wing aircraft available in Galapagos, combined with simultaneous censuses of fixed plots to calibrate the aerial data. Calibration plots could also serve as long-term fixed plots for tracking abundance and reproduction. However, only a small fraction of nesting birds may be visible in aerial imagery, as most nesting and resting birds in the Central Colony were tucked under vegetation. Moreover, the visible fraction may vary with habitat conditions and time of day, and correction factors may be difficult to derive. Therefore, walking surveys may still be needed.

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INSECT POLLINATORS OF *JASMINOCEREUS THOUARSII*, AN ENDEMIC CACTUS OF THE GALAPAGOS ISLANDS

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SUMMARY

Jasminocereus is a columnar cactus endemic to the Galapagos Islands, and is distributed mainly in the lowland arid zones. Its only species, *J. thouarsii*, has several varieties on different islands. Observations of the variety *J. thouarsii* var. *delicatus* on Santa Cruz Island suggested limited recruitment. We therefore studied its floral biology, pollination requirements and seed germination to determine whether recruitment might be limited by seed production or seed quality. Flowers opened in the early morning, from 5h00 to 10h00. No seed was produced by flowers isolated in pollination bags. Pollination was allogamous, mostly brought about by the endemic *Xylocopa darwini* (Hymenoptera: Apidae), followed by the introduced *Acrosticta apicalis* (Diptera) and endemic *Camponotus planus* (Hymenoptera: Formicidae). Seeds germinated well, with the highest germination rate obtained from seeds that were soaked before planting.

RESUMEN

Insectos polinizadores de *Jasminocereus thouarsii*, un cactus endémico de las Islas Galápagos. *Jasminocereus* es un cactus columnar endémico de las Islas Galápagos que se encuentra principalmente en las zonas áridas de baja altitud. Su única especie, *J. thouarsii*, posee algunas variedades en diferentes islas. Observaciones de *J. thouarsii* var. *delicatus* en la Isla Santa Cruz, sugieren que existe una renovación limitada de la población. Por lo tanto, se estudió su biología floral, requerimientos para su polinización y germinación de las semillas para determinar si el reclutamiento podría estar limitado por la producción de semillas o por la calidad de las mismas. Las flores se abrieron por la mañana, entre las 5h00 y las 10h00. Las flores aisladas en bolsas antipolinizadores no produjeron semillas, ya que la polinización es de tipo alógamo, mayormente llevada a cabo por *Xylocopa darwini* (Hymenoptera: Apidae; endémico), seguida por *Acrosticta apicalis* (Diptera; introducida) y *Camponotus planus* (Hymenoptera, Formicidae; endémica). Las semillas germinaron bien, habiéndose obtenido el mayor porcentaje de germinación a partir de semillas que fueron puestas en remojo antes de ser plantadas.

INTRODUCTION

Jasminocereus thouarsii (Weber) Backbg. (Cactaceae) is the only species of the Galapagos endemic genus *Jasminocereus*. It is a columnar cactus distributed in the arid coastal

areas of several islands. It is listed as Near-Threatened (León-Yáñez *et al.* 2010), and preliminary studies have shown that natural regeneration is infrequent (P.J. unpubl.).

Three varieties of *Jasminocereus thouarsii* have been recognized (Wiggins and Porter 1971): var. *sclerocarpus* (K.

Schum.) Anderson & Walkington on Fernandina and Isabela; var. *thouarsii* (Weber) Backbg. on Floreana and San Cristobal; var. *delicatus* (Dawson) Anderson & Walkington on Santa Cruz, Santiago and other smaller islands such as Bartolomé (McMullen 1999). The variety studied here, *J. t.* var. *delicatus*, is a branched columnar cactus up to 7 m tall. It flowers between December and June. Flowers are 6–8 cm in diameter, yellowish with numerous stamens 2 cm long and a stigma of 1–1.5 cm. The reddish purple fruits are 1.5–4.5 cm long and 3.5–4.2 cm across (Wiggins & Porter 1971).

J. thouarsii is listed as Near Threatened (León-Yáñez *et al.* 2010), and preliminary studies have shown that natural regeneration is infrequent (P.J. unpubl.). The species has no asexual reproduction and there is no clear indication of the causes of limited regeneration. Self incompatibility and low seed production have been observed in other cactus species (*e.g.* Mandujano *et al.* 1998, Piña *et al.* 2007), which led us to investigate the reproductive biology of *J. thouarsii*.

Numerous species of columnar cacti are pollinated by bats (Valiente-Banuet *et al.* 2002) but Galapagos bats are exclusively insectivorous (McCracken *et al.* 1997). Previous studies have shown that the endemic carpenter bee *Xylocopa darwini* Cockerell (Hymenoptera: Apidae) is the main pollinator for many Galapagos flowering plants (McMullen 1987). *Opuntia* flowers are visited by finches Geospizinae (B.R. Grant & Grant 1981), which eat pollen (Grant 1996) but no study mentions visits to *Jasminocereus*. Jackson (1993) predicted nocturnal insects (especially moths) as the pollinators of *Jasminocereus*, but the characteristics of the flowers suggest that pollination by the carpenter bee may be more likely.

This paper describes aspects of the reproductive biology of *J. thouarsii*, including the flowering phenology, insect visitors and pollen grain structure, and reports experiments to determine whether the species requires a pollen vector, optimal conditions for seed germination, and the growth rate of seedlings.

METHODS

The study was performed in the dry coastal zone of Santa Cruz Island, Galapagos, Ecuador, in the area surrounding the Charles Darwin Research Station (*c.* 0°44' S, 90°18' W). The climate is tropical semi-arid with an average annual rainfall of 620 mm (CDRS weather station for the period 1982–2002) but with extreme variability due to the El Niño Southern Oscillation that causes most years to have either much higher or lower precipitation (*e.g.* 2768 mm in 1983, 63 mm in 1985). Rainfall in coastal areas is highly seasonal with a cool dry season from July to September (average daily temperatures around 21°C) and a hot wet season from December to April (26–27°C). The study was carried out in 2001 and 2002 during the hot wet season when flowering takes place. The first year of study (2001) was dry, with 293 mm rainfall, the second year (2002)

near average (577 mm). Being located close to the equator, the sun rises within about 30 minutes of 6h00 local time throughout the year

Ten *Jasminocereus* adults were selected in the study area and tagged. Daily flowering phenology of 25 flowers on these plants was observed during two weeks in April in 2001 and 2002, in the middle of the flowering season. For the two plants with the most flowers, eight flowers per plant were selected for study of pollinator visits. Flowers were open between 6h00 and 11h00 only. Three observers identified and counted all visitors to the 16 flowers during the first 20 minutes of each hour from 6h00 to 11h00, for 14 days each year in May 2001 and 2002. Additional night observations were carried out between 18h00 and 22h00 for four nights in 2001. Following these observations, all 16 flowers studied were harvested for collection and description of pollen.

Pollen grains were acetolysed following the protocol of Erdtman (1960) and Kearns & Inouye (1993), and mounted in glycerine jelly for light microscopy. Measurements were made with the light microscope on 25 pollen grains. For scanning electron microscopy, the acetolysed pollen was mounted on cover slips previously attached to aluminium stubs with silver paint, coated with evaporated gold by ion sputtering and examined with a JEOL JSM840 microscope. The terminology used for pollen descriptions follows Punt *et al.* (1994).

On each of five of the ten plants, two flower buds were tagged and enclosed in Hubo “golden magic-mark” pollination bags to test for self pollination. On each of the other five plants, two unenclosed buds were tagged as open pollination controls. Fruits produced were harvested when ripe and seeds were counted.

From each of the five control plants, five additional mature fruits per plant (total 25 fruits) were harvested in June 2001, to obtain 1200 seeds for germination trials. Three replicates of 100 seeds were submitted to each of four treatments: in T1 and T2 seeds were submerged for 24 h in water at a constant temperature of 25 and 60°C respectively and then laid on moist filter paper in petri dishes; in T3 and T4 seeds without prior soaking were laid in petri dishes on humid soil and on moist filter paper respectively. Petri dishes were placed next to a window inside a laboratory with no additional light or heating for four months. When seedlings reached 5 mm in height, they were transplanted to soil and measured monthly until April 2002. Seedlings were watered regularly.

RESULTS

Flowering phenology

During our study, all flowers opened in the morning after 5h30 and closed by 10h00. None opened at night.

Insect visitors

In a total of 800 recorded insect visits during both years, the only three insect species recorded were *Xylocopa*

darwini (54% of visits), the introduced fly *Acrosticta apicalis* Williston (Diptera: Ulidiidae) (34%) and the endemic ant *Camponotus planus* Smith (Formicidae) (12%). For all species, a peak was observed between 7h00 and 7h20. Less than 3% of the visits were between 10h00 and 10h20. No other animal was observed visiting the flowers during the study. No insect was observed visiting the closed flowers during the night. The cumulative number of visits during the morning hours was significantly larger in 2002 than 2001 for the three insect species; the peak was the same each year with an overall average of about two visits per 20-minute observation period (Fig. 1). The pattern of variation in time was similar in both years as indicated by the absence of a year–time interaction in a three way ANOVA (Table 1).

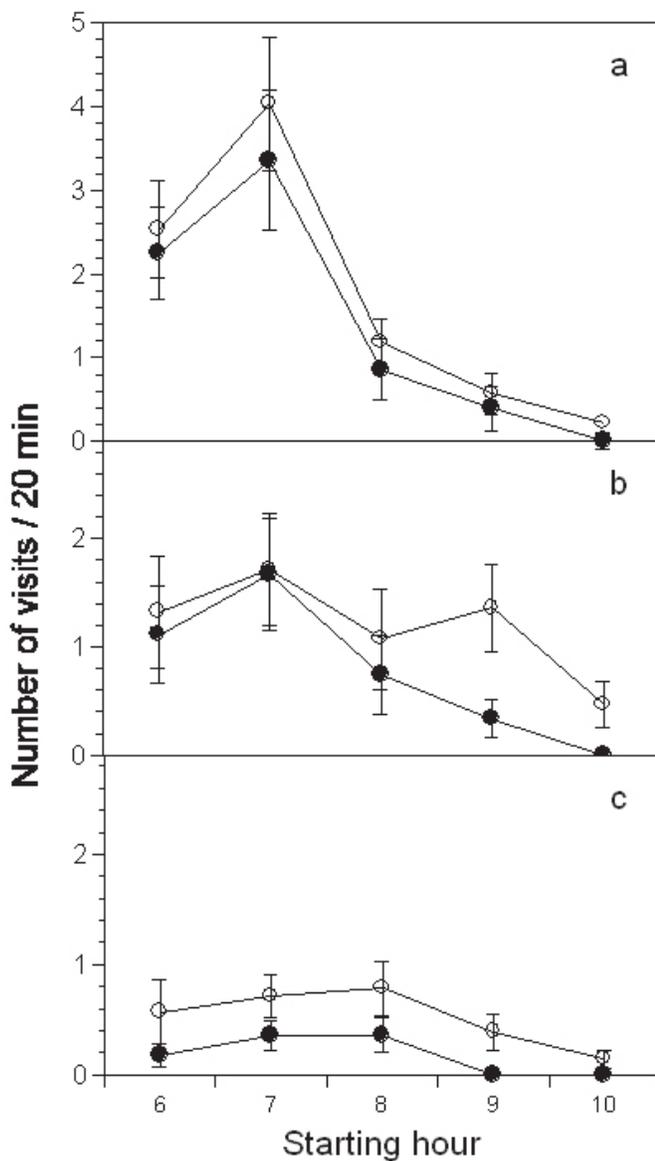


Figure 1. Visits to *Jasminocereus thouarsii* flowers in May 2001 (closed circles) and May 2002 (open circles) by three insect species: a. *Xylocopa darwini*, b. *Acrosticta apicalis*, c. *Camponotus planus*. Data are mean ± SE (n = 28: 14 days x 2 plants).

Table 1. Results of a three way ANOVA for the visits of three insect species to flowers of *J. thouarsii* in 2001 and 2002, and between 6h00 and 10h00.

| Effect | d.f. | F | P |
|--------------|------|------|--------|
| Species | 2 | 25,4 | 0,0000 |
| Year | 1 | 7,11 | 0,0078 |
| Time | 4 | 22,0 | 0,0000 |
| Species.Year | 2 | 0,03 | 0,9662 |
| Species.Time | 8 | 7,10 | 0,0000 |
| Year.Time | 4 | 0,11 | 0,9792 |

Pollen description

Pollen grain morphology was studied in 10 selected plants but only one sample was acetolyzed for scanning electron microphotography. This plant and the acetolyzed pollen sample are deposited in the Charles Darwin Research Station Herbarium as sample CDS 11771. Fresh pollen grains tended to agglomerate due to the presence of fat compounds. Pollen grains (Fig. 2) were trizonocolpate, sometimes trizonocolporoidate, isopolar, radiosymmetric, circular and slightly 3-lobed with convex mesocolpia in polar view and circular to slightly elliptical in equatorial view, from suboblate to prolate-spheroidal. Polar/Equatorial (P/E) axis ratio was 0.85–1.02 (mean 0.96, n = 25 grains), with P = 36–44 (mean 39.6) μm and E = 39–44 (41.4) μm. The apertures were terminal, long and narrow colpi with colpal membrane scabrate to granular, a diffuse pore appearing in the equatorial zone, generally only well appreciable with the light microscope. Exine was 2–3 μm thick, with the sexine being c. three times thicker than the nexine. Infratectum was columellated, tectum perforate, the perforations circular, surrounded by a thick

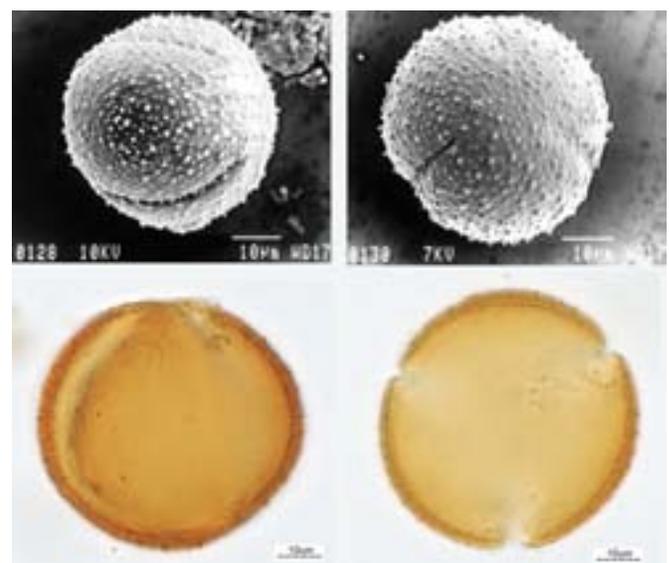


Figure 2. Top, scanning electron micrographs of *Jasminocereus* pollen (left, equatorial view; right, polar view); bottom, light microscope images (left, equatorial view; right, polar view).

border and regularly disposed all around the surface of the pollen grain. As suprastectal elements, we could distinguish dispersal, conical and bulbous microechinae with a wider base and striated surface about 2 μm in diameter and 1 μm high.

Pollination mechanism

None of the flowers enclosed in pollination bags produced fruit. The control flowers all produced fruits that reached about 2 cm long after 15 days. They were ripe and harvested after 22 days. Mean seed production was 325 seeds per fruit (SE 15.3, $n = 10$).

Seed germination

Seed germination was high in all treatments apart from T3 (unsoaked, on soil). Differences among treatments were significant (ANOVA $F_{3,8} = 27.9$, $P < 0.0001$) but the post-hoc Tukey HSD test showed that only the treatment in soil differed from the others (mean 7.3 %, SE 4.6, $n = 3$ in soil vs 54.0 %, SE 3.5, $n = 9$ for the other three treatments, Table 2). Germination started after four days following treatments T1 and T2, after 20 days in T3 and eight days in T4.

Seedling growth

During the growth measurements between June 2001 and April 2002, mortality was high for all treatments, decreasing after month 10. The height (ground to tip) of 11-month old seedlings ranged between 9 and 25 mm. Differences among treatments were significant, with maximum growth for T2 (ANOVA, $F_{3,106} = 4.72$, $P = 0.004$, Table 2).

DISCUSSION

This study presents baseline information that will help to determine factors that may be significant in the recruitment of this endemic species.

Although animals are known to be frequent pollen vectors for columnar cacti (Fleming *et al.* 2001, Clark-Tapia & Molina-Freaner 2004, Ibarra-Cerdeña *et al.* 2005), in Galapagos, where all the bat species are insectivorous, *Jasminocereus* appears adapted to insect pollination. The timing of flower availability (morning opening, closing by 10h30) and the pollen characteristics (sticky, nutritious and large) are indicative of entomophilous pollination. Contrary to what Anderson (2001) mentions, our observations show flowers were closed at night, with no nocturnal pollinators.

Numerous flowering plants in Galapagos rely on one generalist pollinator, the endemic carpenter bee *Xylocopa darwini*, that is known to visit some 60 plant species (Linsley *et al.* 1966, McMullen 1987, 1993). Our observations confirm the importance of this pollinator and represent the first records of insect pollinators for *Jasminocereus* in the Galapagos Islands.

Comparing fruit and seed set of open-pollinated flowers versus flowers that were isolated from pollinators, we conclude that *Jasminocereus* is not capable of autonomous self-pollination. Of 52 Galapagos plant species studied by McMullen (1987), 40 were self-compatible. *Jasminocereus* may be self-compatible (autogamous), but requires a pollen vector.

In the case of *Jasminocereus*, the need for a vector could well be a cause for the limited fruit production of isolated plants. For plants receiving adequate pollinator visits to produce fruits however, viable seed production per fruit appears to be sufficient for this not to be a limiting factor in the regeneration of the species. However, the low germination success for seeds planted directly into soil, a drier medium than filter paper in petri dishes, suggests that germination in the field may be rare, perhaps associated with high rainfall events that occur with El Niño.

Another important factor to take into account, and not measured here, is loss of flowers and fruit to herbivores. Finches and mockingbirds *Nesomimus* spp. eat and destroy flowers and flower parts of some cacti (P.R. Grant & Grant 1979, B.R. Grant & Grant 1981, Millington & Grant 1983, Grant 1996) as do lava lizards *Microlophus* spp. (C. Buddenhagen pers. comm.); this may limit seed production in some cases.

Information on the reproductive biology of endemic species is a critical step to understanding factors that may limit their populations. The life history strategies of long-lived species such as *Jasminocereus* may be especially difficult to understand, as they may be highly adapted to irregular El Niño Southern Oscillation events. Thus long term study is essential for gathering the information necessary to set appropriate conservation priorities.

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Table 2. *Jasminocereus thouarsii* germination trial results for four treatments (see Methods). Data are mean \pm SE (n).

| | T1 | T2 | T3 | T4 |
|---|---------------------|---------------------|--------------------|---------------------|
| Final germination % | 52.0 \pm 10.2 (3) | 47.3 \pm 8.1 (3) | 7.3 \pm 3.0 (3) | 66.7 \pm 8.6 (3) |
| Seedling mortality % | 43 | 48 | 30 | 47 |
| Final growth in length after 11 months (mm) | 13.3 \pm 1.8 (36) | 16.4 \pm 4.9 (29) | 14.2 \pm 0.4 (7) | 14.4 \pm 3.1 (38) |

contribution to pollen studies in Galapagos. We thank Conley K. McMullen, Washington Tapia, Chris Buddenhagen and Rachel Atkinson for their valuable comments on the document. This work was accomplished with financial support from the U.K. Government's Darwin Initiative. This is contribution number 2019 of the Charles Darwin Foundation for the Galapagos Islands.

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CHARACTERIZING THE GALAPAGOS TERRESTRIAL CLIMATE IN THE FACE OF GLOBAL CLIMATE CHANGE

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SUMMARY

The position of Galapagos in the Eastern Pacific gives it a unique seasonal climate that is atypical of other equatorial oceanic islands. Conditions are influenced by the interaction of ocean currents and winds, governed by the movement of the Inter-Tropical Convergence Zone, and by the periodic Pacific-wide El Niño Southern Oscillation. Weather data from 1959 to 2009 on Santa Cruz Island show that the hot season prevails from January to May, characterized by elevated sea and air temperatures and highly variable rainfall. During the cool season, from June to December, cooler temperatures and a stratus cloud layer persist, resulting in relatively consistent precipitation in the humid highlands and almost none in the dry lowlands. Hot season rainfall totals are strongly correlated with sea surface temperature, whereas cool season rainfall totals are consistent from year to year, and not so closely correlated with sea surface temperature. Seasonal rainfall totals from ten locations on six islands show correlations among the majority of sites for the hot season but fewer for the cool season, one exception being the correlation between sites on Santa Cruz Island, all of which receive at least some cool-season precipitation. Biological productivity in the dry lowlands is primarily influenced by the variable hot-season rainfall. The humid highlands are maintained by more consistent precipitation every year in the cool season, but are also affected by conditions during the hot season. We suggest that the dry zone is vulnerable to a warmer, wetter climate which would favour invasive species and thereby doubly threaten arid-adapted endemic species. Potential climate change impacts on the already-invaded and more species-rich humid highlands are harder to predict due to our lack of understanding of cool-season precipitation patterns. In order to understand spatial climate variability in Galapagos better, there remains a need for meteorological data with a greater spatial spread throughout the islands, especially at higher altitudes.

RESUMEN

Describiendo el clima terrestre de Galápagos a la luz del cambio climático global. La posición de Galápagos en el Pacífico del Este le da un clima estacional único atípico en otras islas oceánicas ecuatoriales. Estas condiciones están influenciadas por la interacción entre las corrientes oceánicas y los vientos, regidas por el movimiento de la Zona de Convergencia Intertropical y por el fenómeno periódico a lo largo del Pacífico de El Niño Oscilación del Sur. Datos del clima en la Isla Santa Cruz desde 1959 hasta 2009 muestran que la estación cálida prevalece de Enero a Mayo, caracterizada por temperaturas elevadas del mar y del aire y por alta variabilidad de la precipitación. Durante la estación fría, de Junio a Diciembre, temperaturas más bajas y una capa de nubes estratos persisten, resultando en una precipitación relativamente consistente en las zonas altas húmedas y prácticamente ninguna en las zonas bajas secas. La precipitación total de la estación cálida se correlaciona fuertemente con la temperatura de la superficie del mar, mientras que la precipitación total durante la estación fría es consistente de año a año, y no se correlaciona tan cercanamente con la temperatura de la superficie del mar. La precipitación total estacional de diez locaciones en seis islas muestran correlaciones entre la mayoría de los sitios para la estación cálida pero hay menos correlaciones para la estación fría, siendo una excepción la correlación entre sitios en la Isla Santa Cruz, de los cuales todos reciben al menos alguna precipitación de estación fría. La productividad biológica en las zonas bajas secas está primordialmente influida por la precipitación variable de la estación cálida. Las zonas altas húmedas son mantenidas por precipitaciones más consistentes cada año en la estación fría, pero también son afectadas por las condiciones durante la estación cálida. Sugerimos que la zona seca es vulnerable a un clima más caliente y más húmedo, lo cual podría favorecer especies invasoras y por lo tanto amenazar doblemente las especies endémicas adaptadas a las condiciones secas. El impacto potencial del cambio climático en las zonas altas húmedas más ricas en especies y ya invadidas es más difícil de predecir debido a nuestra falta de comprensión de los patrones de precipitación de la estación fría. Para poder comprender mejor la variabilidad climática espacial en Galápagos, queda la necesidad por datos meteorológicos de mayor amplitud espacial a lo largo de las islas, en especial a mayores altitudes.

INTRODUCTION

Located on the equator, 1000 km west of the coast of South America, the Galapagos Islands have a unique climate influenced by the interaction of oceanic currents and winds. Early visitors to the archipelago noted the comparative cool of the climate in comparison with other places on the equator (Dampier 1729, Darwin 1845), the occurrence of two distinct seasons (Dampier 1729), and the presence of a humid “luxuriant vegetation” zone in the uplands, compared to the “sterile” lowlands (Darwin 1845). These features are still the most notable of the Galapagos climate, along with the formidable periodic influence of hot, wet El Niño years and their dry La Niña counterpart (Snell & Rea 1999). With the benefit of modern climatic records a deeper understanding of the Galapagos climate is possible.

Here, we provide a climate analysis preceded by a review of climate reporting and climate mechanisms as contextual information. With current concern for global climate change and its impacts, this knowledge is necessary to predict potential consequences for terrestrial biodiversity in Galapagos. Our analysis incorporates previously unpublished data for the last decade. We use Santa Cruz meteorological data to characterize the climate because it contains continuous and parallel long term data from both lowland and highland sites. We use data from 1959 to 2009 to describe climate features throughout the year and to reveal trends over time. We differentiate two seasons, hot and cool, each of which has distinct influences on biological productivity and hence biodiversity. We also use rainfall data from an additional eight stations on six islands to improve understanding of the spatial distribution of rainfall throughout the archipelago. We discuss potential biodiversity changes in each of the two main climatic zones as a result of global climate change.

GALAPAGOS CLIMATE REVIEW

Climate reporting

Alpert (1946) established the first systematic collection of climatic data on the islands, at a weather station on the island of Baltra during the Second World War. His observations formed the basis of a seminal paper on the climate of Galapagos (Alpert 1963). Palmer & Pyle (1966) wrote about the dry climate of Galapagos in relation to their geographical position and oceanographic conditions. Colinvaux (1968, 1972, 1984) used lake and bog cores to show that the Galapagos climate has been primarily dry for thousands of years, punctuated with some wetter events. This and other palaeoclimatic research has been reviewed by Bush *et al.* (2010).

These early publications contained very little quantitative information (P.R. Grant & Boag 1980) but this changed when Hamann (1979) used data from 14 stations on five islands to construct climatic diagrams and relate

climate to vegetation types. An excellent report on a range of climate measurements from 1964–81 at seven of these stations was presented by Nieuwolt (1991), noting the seasonal climate that is atypical for equatorial locations. Nieuwolt observed the year-round suitability of the highlands for agriculture but acknowledged that rainfall irregularity is a limiting factor in the hot season. The most comprehensive analysis of the existing weather data was carried out by Huttel (1995), including data from some of the same stations as Hamann, for a total of 14 stations on six islands, all registered with the national meteorological institute (INAMHI) network but most of them no longer in operation, and from temporal subsets of the period 1950–87. Huttel (1995) identified three rainfall “vectors” for coastal, transition and highland zones, and noted the lack of data between the coast and 170 m altitude, and above 600 m. Following the 1997–8 El Niño event, Snell & Rea (1999) analyzed the trends in data from the Charles Darwin Research Station and Bellavista, in relation to the occurrence of El Niño events.

Climate measurements have also been important in other studies, especially in relation to finches (*e.g.* P.R. Grant & Boag 1980, P.R. Grant 1985, P.R. Grant & Grant 1996), vegetation (Hamann 1979, Jäger *et al.* 2009), hydrology (Navarro Latorre *et al.* 1991, d’Ozouville 2007) and natural resource management (d’Ozouville 2008).

Climate mechanisms

The Galapagos climate is controlled by the interaction of oceanic currents that surround the islands and the predominant trade winds from the southeast. The influence of the currents and winds is governed on an intra-annual basis by the north-south migration of the Inter-Tropical Convergence Zone (ITCZ), a warm band of deep convection that shifts from 10°N during the northern hemisphere summer to 3°N during the northern winter (Sachs *et al.* 2009). For the majority of the year the ITCZ is well north of Galapagos, and the southeast trade winds blow across Galapagos, bringing with them air cooled by the cold, upwelled waters to the south (Alpert 1946, Colinvaux 1984). When the ITCZ migrates southward, closer to Galapagos, the archipelago is almost in the doldrums; the trade winds are reduced, warmer ocean currents from the north arrive, and conditions in the archipelago are tropical (Alpert 1946).

This intra-annual ITCZ migration gives rise to the two seasons which characterize the Galapagos climate: a hot season and a cool season (Hamann 1979, Itow 2003). These seasons have in the past been referred to as wet and dry respectively (*e.g.* Alpert 1946, Palmer & Pyle 1966, Colinvaux & Schofield 1976, P.R. Grant & Boag 1980), as the vast dry lowlands of the archipelago only receive substantial rain in the hot season (except in El Niño years). The wet/dry nomenclature can however be misleading, because the highlands of the islands are typically wetter during the cool season (Hamann 1979) and the lowlands can also be very dry during the hot season. The hot season

is characterized by convection, resulting in orographic rainfall that increases with altitude (Snell & Rea 1999). The cool season is characterized by an inversion layer, when air cooled by the ocean surface is trapped below warmer air, creating condensation just below where the two air masses meet (Colinvaux 1984), especially on the windward side of the islands where air is pushed up against the land (Hamann 1979) (Figs 1 & 2). This condensation usually occurs above 250 m altitude and creates extensive stratus clouds, often down to ground-level, locally called *garúa* (Hamann 1979, Colinvaux 1984, Nieuwolt 1991). These clouds result in two forms of precipitation; vertical (rainfall) and occult, the latter consisting of fog that condenses on vegetation and drips or runs down to the ground. In Galapagos, occult precipitation can significantly increase the total precipitation amount under dense vegetation (Jäger *et al.* 2009). Data used in this analysis do not include occult precipitation because the rain gauges are not situated beneath vegetation.

A Pacific-wide phenomenon also plays an important role in Galapagos climate: El Niño Southern Oscillation (ENSO). The warm phase of ENSO is referred to as El Niño and the cold phase as La Niña. During El Niño events the eastern Pacific experiences high sea surface temperature, weakening of the southeast trade winds and deepening of the thermocline; all of which strengthen conditions associated with the southward displacement of the ITCZ. The effects in Galapagos include high air temperatures, torrential rainfall and a longer than usual hot season (Snell & Rea 1999). La Niña events bring colder than normal conditions and drought, although the effects of ENSO on cool season climate dynamics are not well understood (Sachs & Ladd 2010). Palaeoclimatologists have used coral cores and lake or bog sediments to show that ENSO fluctuations have been occurring in the archipelago for hundreds to thousands of years (Dunbar *et al.* 1994, Riedinger *et al.* 2002, Conroy *et al.* 2009).

ENSO events (or years) have been defined in many different ways that include either or both atmospheric and oceanographic indices (*e.g.* Smith & Sardeshmukh 2000). Consequently, lists of events are not consistent with each other or for different regions, nor with effects experienced in Galapagos, especially for less intense events. Also, there are inconsistencies in the listing of years in which events occurred because some El Niño events persist for two consecutive hot seasons, with a cool season in between, while others begin in November or December and extend through a wet season until June the following year. Recent El Niño events in Galapagos include 1975–6, 1982–3, 1986–7, 1993–4 and 1997–8 (Snell & Rea 1999). The very strong events of 1982–3 and 1997–8 had dramatic effects on Galapagos ecosystems (Robinson & del Pino 1985, Snell & Rea 1999, Vargas *et al.* 2006). Within the last decade, El Niño events have caused high rainfall in the hot seasons of 2002 and 2010. High rainfall in 2008 was not associated with an El Niño event.

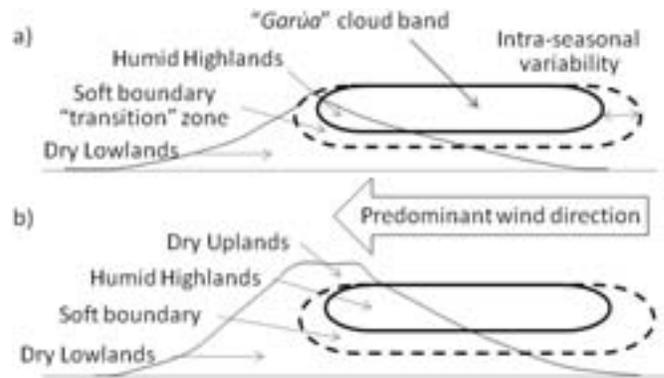


Figure 1. Galapagos landscapes with cool-season cloud and the resulting climatic zonation: a) islands of intermediate height (Santa Cruz, San Cristóbal, Floreana, Santiago, Pinzón, Pinta); b) the six volcanoes of Isabela and Fernandina islands.

Climate zones

The stratus cloud layer that dominates each cool season has led to a climatic zonation from the dry lowlands to the humid highlands, and on the higher islands to a third zone, the dry uplands (Fig. 1). Whilst these climatic zones have not been mapped, they correspond to naturally occurring semi-arid and humid vegetation zones as described by Hamann (1979) and mapped by Huttel (1986) (Fig. 3). We refer to these as climatic zones rather than vegetation zones, partly because the natural vegetation zonation is more complex and is a response to these climatic factors, and partly because the natural vegetation zonation has been completely altered by anthropogenic change on the inhabited islands (Snell *et al.* 2002, Watson *et al.* 2009), whilst the climatic drivers have generally been maintained.

The soft boundary between the humid and dry climatic zones (Fig. 1) matches the vegetation "Transition Zone" of Wiggins & Porter (1971) (Fig. 3), which has been characterized in terms of climate and vegetation (see also

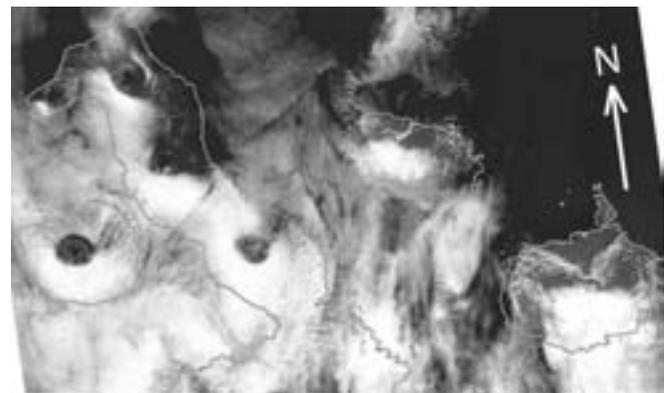


Figure 2. Satellite imagery showing typical cool-season stratus cloud formation over central-west Galapagos on 25 Nov 2009. Source: Landsat 5, USGS <<http://edcns17.cr.usgs.gov/cgi-bin/EarthExplorer>>.

and Bellavista (0°41'46.53''S, 90°19'37.20''W) at 194 m a.s.l. (Fig. 3). Many of the data used here are available for download at <www.darwinfoundation.org>. These locations are used to represent the dry lowlands and the humid highlands respectively, although each is located at the lower altitudinal limit of these two climatic zones respectively.

To understand temporal variation within years, we describe the annual variation in key climate variables by charting monthly averages using available data for the two stations. The variables used are sea surface temperature (SST), total rainfall, number of rain days (defined as days where rainfall >0), air temperature, humidity, sunshine hours and wind (strength and direction). For rainfall and rain days we used median instead of mean, as recommended by Nieuwolt (1991), due to the highly skewed variation in rainfall in many months. All data were collected daily, and were summarized into charts of monthly averages or totals using Microsoft Excel.

For SST, the variation in recordings for each month is indicated by standard deviation, and for rainfall by the interquartile range. Seasonal trends in other climate variables are not presented here as they did not show any distinct patterns. No different treatment was carried out for El Niño years.

At each station, data were collected on different climatic variables and over different periods. At ECCD data on most variables were available from January 1965 to October 2009, except sunshine hours, which began in January 1978, and wind, which began in July 1987 and terminated in July 2009. At Bellavista, data on most variables were available from July 1987 to September 2009, except sunshine hours, which began in April 1994. Some daily data are missing for wind and sunshine at both locations. SST was recorded at the coast in a bucket of water pulled from the sea. Air temperature was recorded in shade 2 m above the ground; we use daily minimum and maximum. Daily rainfall is the sum of measurements taken at 12h00, 18h00 and 6h00 the following day, in a rain gauge 1.5 m above the ground. All data were recorded manually.

To define the general timing of seasons we determined in which month each season had begun for all years 1965–2009, using SST. We defined the transition between hot and cool seasons as the month in which the mean SST reached the midpoint between the highest (or lowest) monthly mean SST of the hot (or cool) season and the subsequent lowest (or highest) monthly mean SST of the following cool (or hot) season. From this we determined the season in which each month most frequently occurred, and therefore a predominant annual pattern of the seasons.

We summed rainfall data and averaged SST for each seasonal period (hot = January–May, cool = June–December) and over the whole year, each year, at ECCD and Bellavista. The seasonal SST averages and rainfall totals were plotted as time series to assess trends, and the

rainfall totals were also used to compute the median, minimum and maximum seasonal and annual rainfall at the two stations, identifying in which season the larger proportion of the rainfall fell at each. We also tested for a correlation between seasonal and annual rainfall totals and SST averages. We identified four “outlier” years, of exceptional rainfall in the cool season: all years in which El Niño events extended into the normal cool season months (1972, 1982, 1983 and 1997). These years are unrepresentative of cool season rainfall and were therefore excluded from some analyses, as mentioned below. Although hot season rainfall totals were also exceptional in El Niño years, none of these are considered outliers because they form part of a continuous trend of hot season rainfall in relation to SST (see below, Fig. 6).

To understand the spatial variation of rainfall across the archipelago, we used data from an additional eight locations with records from a minimum of six years. These sites (and the years of available data) are: Baltra (1999–2008), Corazon Verde (1970–99 except 1974 and 1995), Daphne (1976–2008), Genovesa (1978–88), La Soledad (1997–2007), Miconia (1996–2005), Radio Sonda (1977–83; 2002–8), and Santa Rosa (2003–8) (Fig. 3). These stations represent six islands, with half of the sites located in the humid or transition zone and the other half in the dry zone. Most data were provided as daily rainfall totals by the Charles Darwin Research Station. Data from Genovesa were obtained from B.R. Grant & Grant (1989) in monthly totals for January–May in all years except 1982–3 (Jan–May 1982 and December 1982 to July 1983). Daphne data were provided by P. & R. Grant (pers. comm.) as annual totals, but are interpreted here as hot season rainfall only, because cool season rainfall on that island is negligible (P. Grant pers. comm.).

Rainfall data were summed to produce seasonal totals for each of the ten locations, using the above-defined periods for the seasons. To examine matches between locations for each of the hot and cool seasons, data were plotted as time series. Correlation coefficients were generated (in Microsoft Excel) to compare rainfall at each location with each of the other locations, for all pairs of data sets which had at least five years of concurrent data. For the cool season, four outlier years were excluded, as explained above. To understand spatial variation within a single island, some daily rainfall data of extreme rainfall events were compared between ECCD in the lowlands and Bellavista in the highlands.

Rainfall isohyets were created for each of the hot and cool seasons for Santa Cruz Island, using rainfall records for the four stations on this island plus those on Daphne and Baltra, along with data from three additional highland sites on Santa Cruz (S. Henderson pers. comm., d'Ozouville 2007, Jäger *et al.* 2009) and existing vegetation mapping (INGALA *et al.* 1989). We performed a manual interpolation of median seasonal rainfall totals, guided by vegetation zone boundaries and altitude.

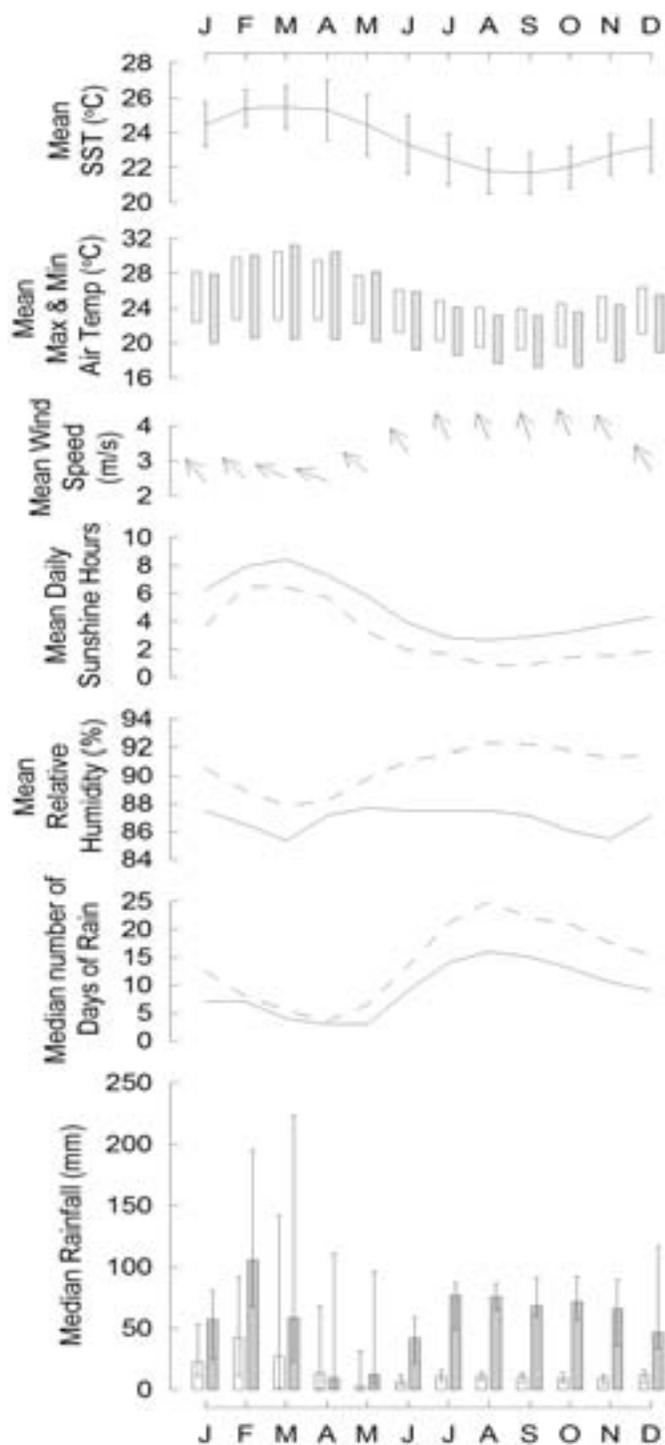


Figure 4. Annual variation in climate variables in Galapagos over the period of data availability. SST are expressed as monthly means \pm S.D., recorded at ECCD. Monthly air temperature bars indicate mean daily minimum and maximum for ECCD (white) and Bellavista (grey). Wind speed is the monthly mean (base of arrow) of daily records at ECCD (median of 24 measurements per day), with arrows showing mean direction for each month. Sunshine and humidity are expressed as monthly means of daily records, and number of rain days as the median of all years, for ECCD (solid line) and Bellavista (dotted line). Rainfall bars show median monthly totals for ECCD (white) and Bellavista (grey), with error bars depicting the interquartile range.

Results

Defining the seasons. Data from ECCD and Bellavista show two distinct periods of the year, hot and cool, driven by sea surface temperatures that were higher in the first half of the year (Fig. 4). The hot season generally began in January, peaked in February and March, and finished in May (Fig. 5). However, it occasionally started as early as November or finished as late as July. The cool season thus generally began in June, peaked in August–October and finished in December (Fig. 5). Occasionally, it started as early as April and finished as late as the following January. For the analyses below, we define the seasons as January–May for the hot season, and June–December for the cool season.

Annual variation at ECCD and Bellavista. Air temperatures were also higher in the hot season than in the cool season. Daily maxima were generally 5°C warmer than the minima, except in the sunnier months of February–April when daytime maxima were an additional 3–9°C higher. In general, temperatures at Bellavista were lower than at ECCD, with daily minima being usually 2°C lower in most months of the year. Only during the hot season months of February–May were average daily maxima about 1°C higher in Bellavista than at ECCD.

During the hot season, daily median wind speed averaged $c. 2.4 \text{ m.s}^{-1}$ and wind direction was very variable. In the cool season, daily median speed averaged highest (3.7 m.s^{-1}) in October and winds came from the south-southeast with little variability.

Sunshine hours per day were greater during the hot season than the cool season. More sunshine hours were registered at ECCD than at Bellavista throughout the year.

Humidity was consistently high throughout the year in both stations, but dropped slightly in March–April, and at ECCD again in November.

Rainfall was extremely variable in the hot season at both stations. Peak median rainfall occurred in February in both locations, although zero monthly rainfall was sometimes experienced at ECCD during February–June, and in Bellavista from March to May. Rainfall in Bellavista was higher than ECCD throughout the year, but particularly in the cool season, when Bellavista received $c. 70 \text{ mm}$

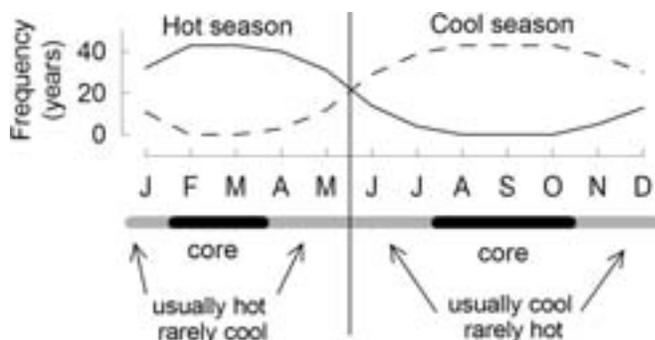


Figure 5. Frequency of the Galapagos hot and cool seasons occurring in each month of the year, based on SST.

per month and ECCD c. 10 mm per month. In the cool season, the amount of rainfall was fairly consistent from month to month and year to year.

At both stations, the median number of rain days per month was lower in the hot season than in the cool season. The peak month for rain days at both locations was August. The month with fewest rain days was May at ECCD, April at Bellavista. Number of rain days was not closely related to the amount of rainfall. Rain days at ECCD during the cool season typically produced < 2 mm of precipitation (> 80 % of records), but rain days in the hot season often produced > 5 mm (> 40 % of records), and sometimes considerably more: there are ten records of days with > 100 mm of rainfall at ECCD, all in the hot season.

Median annual rainfall was three times higher in Bellavista than at ECCD (Table 1). At ECCD, the majority of the median annual rainfall occurred in the hot season (Table 1). In very dry years, hot-season rainfall was far below the median and often far below the usual hot-season proportion of the annual total; for example, in 1985 only 5 mm of rain was recorded during the hot season at ECCD, out of a total of 64 mm that year. Conversely in Bellavista, more of the annual precipitation occurred in the cool season (Table 1).

Rainfall at ECCD and Bellavista was significantly positively correlated with SST in the hot season, with no obvious outlier years ($r = 0.86$ and 0.82 respectively; $P < 0.001$; Fig. 6a). In the cool season, there was a weaker correlation at both locations ($r = 0.65$ and 0.78 respectively; $P < 0.001$) and when we excluded the obvious cool-season outlier years (1972, 1982, 1983 and 1997), that corresponded to El Niño events in which hot season conditions extended into normally cool-season months, the correlation was further weakened, though still significant ($r = 0.48$ and 0.45 , $P = 0.002$ and 0.040 respectively; Fig. 6b).

Trends at ECCD. The ECCD time series of monthly rainfall and SST from 1965 showed the high variability of rainfall in the lowland zone, with periods of high rainfall corresponding to sustained high SST (Fig. 7). Obvious peaks in hot season rainfall coincided with years of high SST, especially 1983 and 1998 (two extreme El Niño events), when rainfall was high and sustained over many months.

Table 1. Summary rainfall statistics (mm) for ECCD and Bellavista (extreme years given in parentheses).

| | | ECCD | Bellavista |
|-------------|---------|------------------|--------------------------|
| Annual | median | 277 | 813 |
| | minimum | 64 (1985) | 448 (1988) |
| | maximum | 2769 (1983) | 2666 (1997) ¹ |
| Hot season | median | 196 ² | 351 |
| Cool season | median | 81 | 462 ³ |

¹ Bellavista records began in 1988; rainfall might have been higher in the El Niño year of 1983.

² 71% of annual.

³ 57% of annual.

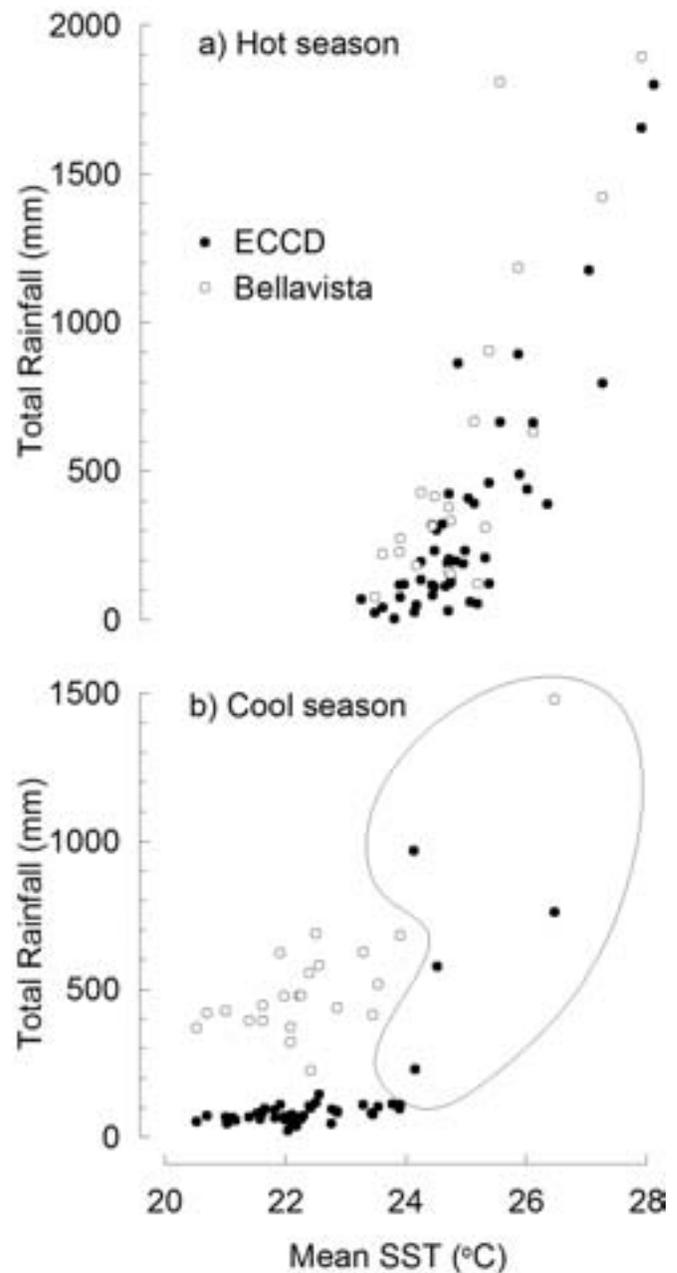


Figure 6. Scatter plot of SST and rainfall in each season at two locations. Obvious outlier years here (circled) are associated with El Niño events that extended into the normal cool season months in 1972, 1982, 1983 and 1997.

Spatial variation. Seasonal rainfall totals appeared to show similar year-to-year patterns at all recording stations in both seasons (Fig. 8). For the hot season, whole-season rainfall at most stations correlated strongly and significantly with most others. Correlation coefficients > 0.77 ($P < 0.05$) existed for 29 out of 35 possible station pairs (83%), with most (19) of these very strong ($r > 0.97$, $P < 0.001$). The exceptions were: Miconia not correlated with Baltra, and Santa Rosa not correlated with any other site except Radio Sonda, perhaps due to the shorter time-span of the Santa Rosa dataset ($n = 6$; all others $n > 9$). For the cool season,

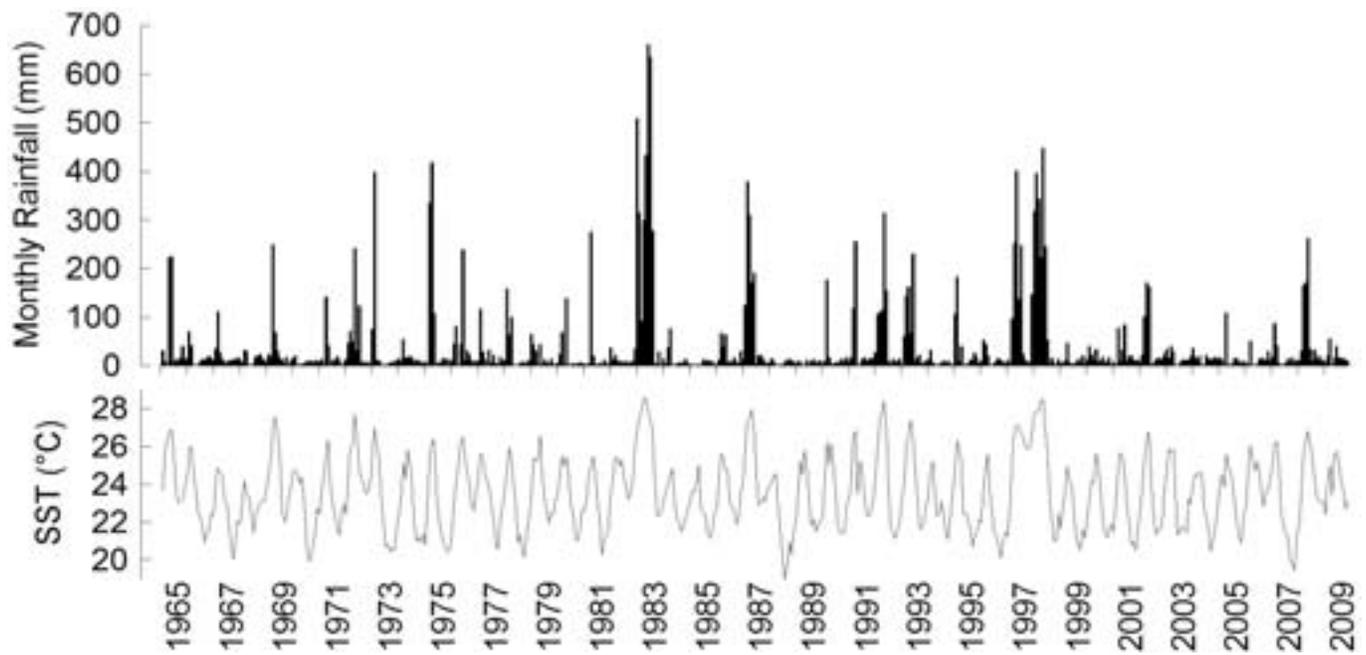


Figure 7. Trends in rainfall (monthly totals) and SST (monthly means) at ECCD, since records began in January 1965 until December 2008.

with the four outlier years excluded, there were fewer correlations among sites. Only nine pairs of 21 possible combinations (43 %) were correlated ($r > 0.44$; $P < 0.05$), including sites on Santa Cruz Island (Bellavista correlated with ECCD, Santa Rosa and Miconia; ECCD correlated with Santa Rosa). Also, Radio Sonda correlated with ECCD, Bellavista, Santa Rosa and Baltra, while Corazon Verde correlated with ECCD. Thus, in the cool season, correlations appear to exist mainly within a single island, or perhaps where concurrent datasets span longer periods.

Rainfall during the hot season, whilst correlated among locations for the seasonal totals, was localized in terms of individual events. This is illustrated by the rainfall during 2008, a year in which the SST was relatively normal, yet Bellavista received 1808 mm (Fig. 6a). This exceptionally high total was due to the three days of highest rainfall on record at Bellavista: 7, 8 and 12 March, with 224, 280 and 490 mm respectively (total 994 mm). On those days, rainfall at ECCD was unexceptional (5, 12, and 0 mm respectively), whereas high rainfall was experienced

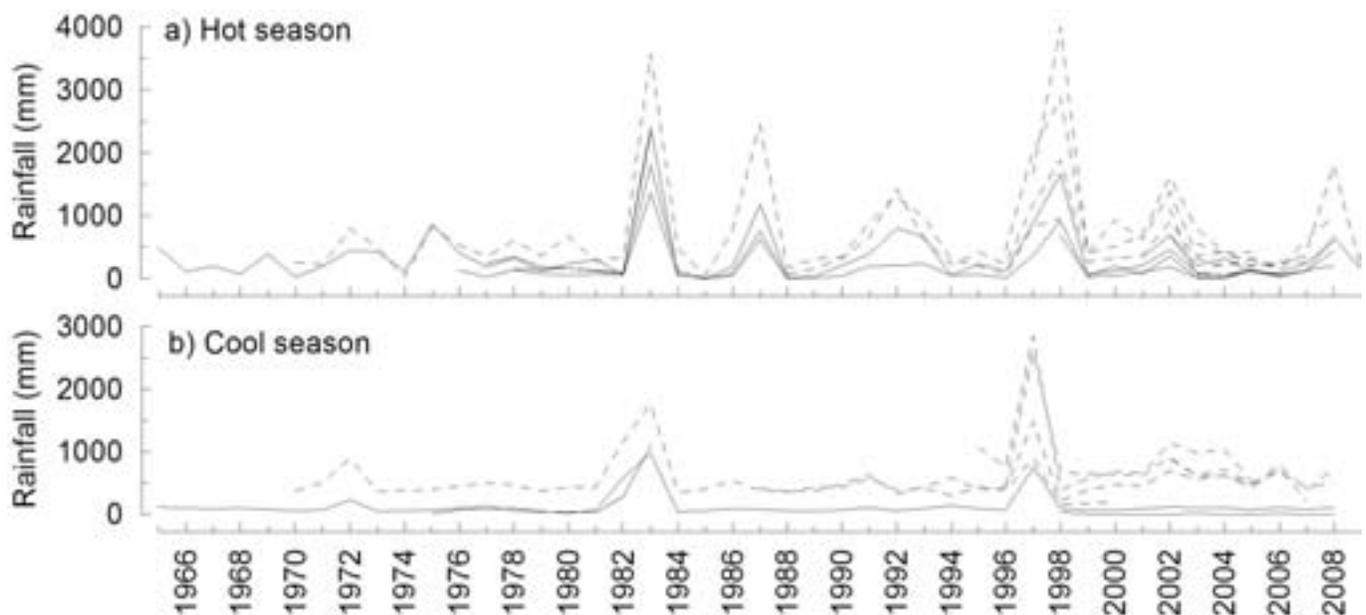


Figure 8. Seasonal trends in total rainfall at lowland (solid lines) and highland (dotted lines) sites for the hot and cool seasons.

on 9 March (55 mm), 3 April (94 mm) and 16 April (62 mm), when rainfall in Bellavista was 6, 74, and 21 mm respectively.

Isohyet maps (Fig. 9) for Santa Cruz Island show increasing rainfall with altitude in both seasons. Although constructed from limited data, this representation improves on previous maps (Navarro Latorre *et al.* 1991, d'Ozouville 2007). Further improvement should take into account occult precipitation during the cool season, and a greater spatial spread of rainfall recordings.

DISCUSSION

Synthesis

The local oceanic and atmospheric conditions result in two distinct annual seasons in Galapagos, which is atypical of equatorial locations (Nieuwolt 1991). During January to May, when the ITCZ is at its southern limit, close to Galapagos, hot conditions prevail. SST and air temperatures are at their annual peak, winds are mild and predominantly from the ESE (although direction is variable), and most days are sunny (Fig. 4). Rainfall is convective and highly variable, with recorded monthly totals from 0–660 mm at ECCD in the lowlands, and 0–1263 mm at Bellavista in the highlands. Convective storms are often small and short, missing one area while deluging another nearby. Rainfall totals are strongly positively correlated with average SST in the hot season, and also among sites throughout the archipelago. From June to December, when the ITCZ lies further north, cooler conditions predominate, with consistent, cool, southeast trade winds, lower SSTs and air temperatures, and persistent stratus clouds (*garúa*) (Fig. 2) that wet the

highlands while the lowlands remain dry. Rainfall in the cool season is more consistent from year to year and month to month, with monthly totals of around 10 mm at ECCD in the lowlands and 67 mm at Bellavista in the highlands, where it rains almost every day. Total rainfall is only weakly correlated with average SST for the cool season, and there are fewer correlations among sites throughout the archipelago.

ENSO events can alter the length and intensity of the seasons; in particular El Niño events lengthen and intensify the hot season, sometimes to the previous November or December or extending into June or July. This can upset cool season trends, and years identified as cool season outliers (1972, 1982, 1983, 1997) all match El Niño events as defined by Smith & Sardeshmukh (2000).

No obvious long-term trends in SST or rainfall are apparent during the period 1965–2009, which might be expected to be associated with global climate change. This may be partly due to the strength of ENSO influence, which provides so much noise that it potentially obscures signal. Records for this period show a significant positive correlation between SST and rainfall, although this is only strong in the hot season. A correlation of rainfall with SST in Galapagos has previously been noted (Houvenaghel 1974), presumably using annual rainfall totals from coastal data, where cool season rainfall contributes little to annual totals. Our findings that, apart from major El Niño years, cool season rainfall is consistent from year to year, only weakly correlated with SST and not correlated between locations except within the highland zone of a single island, beg questions about the drivers of the cool season *garúa* (see also Bush *et al.*, Sachs & Ladd 2010).

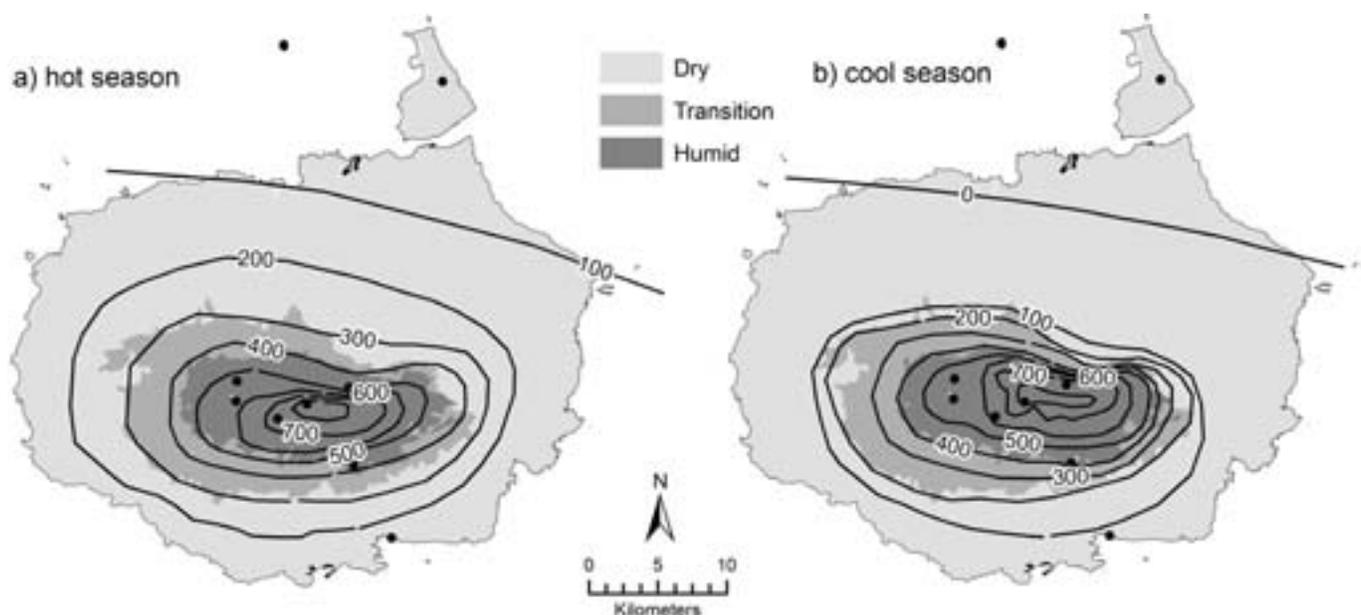


Figure 9. Isohyets for total seasonal rainfall on Santa Cruz Island (mm) for the (a) hot season and (b) cool season. Dots indicate the locations of stations whose data was used to develop these isohyets.

Differences in all climate variables are apparent between the lowlands and highlands. Rainfall is greater in the highlands throughout the year, and this difference is most pronounced during the cool season when rainfall in the lowlands is minimal. However, rainfall is likely to decrease above 800 m, at least in the cool season when the stratus cloud lies below this altitude, which accounts for the presence of a further dry zone on the tops of the higher volcanoes (Huttel 1986). We do not know of any rainfall measurements in this dry upland zone. The decreasing temperature gradient from the lowlands to the highlands is consistent with the results of d'Ozouville (2007), who calculated an average gradient throughout the year of -0.8°C per 100 m altitude on Santa Cruz from 0–855 m. This is steeper than the *c.* -0.5°C per 100 m gradient expected in the humid tropics due to the adiabatic lapse rate (Bush & Silman 2004). Considering that the highlands receive < 3 h of sunshine per day in the cool season and < 6 h per day in the hot season, there may be a significant cooling effect from cloud-shadow in the highlands, especially during the cool season. The slightly higher maximum temperatures in Bellavista compared to ECCD during the hot months of February–May are not consistent with the annual means or with expected adiabatic lapse rates. Whilst our results do not suggest any clear causation, we propose that this may be due to the cooling effect of the ocean on ECCD temperatures, as this station is situated only 20 m from the sea.

While monthly rainfall totals are variable between locations in Galapagos, as observed by Nieuwolt (1991), we show that hot season rainfall totals are correlated among locations throughout the archipelago. Whilst cool season rainfall appears to be relatively constant from year to year in all locations, it is largely not correlated among locations. Notable exceptions are the correlations between sites within Santa Cruz Island, perhaps suggesting an influence of individual island topography on cool season precipitation.

Climate change

Precipitation is recognized as the primary driver of terrestrial biological productivity in Galapagos (Nieuwolt 1991), so changes to it could induce changes in native species distributions and agricultural productivity. The local effects of global climate change may influence precipitation amount, periodicity, and intensity. Given the varying climate mechanisms at work in Galapagos, the effects are likely to be different in each season (Table 2).

Given our understanding of the Galapagos seasons and their manifestations in the lowland and highland zones, we know that the unpredictable hot season rainfall is important for lowland productivity (Porter 1979), and consistent cool season *garúa* precipitation is the major driver of productivity in the humid highlands. Therefore, the two broad climatic zones in Galapagos will likely not respond similarly to global climate change, inducing a new source of heterogeneity that may or may not favour the continued existence of vulnerable organisms. The large lowland zone, with its peculiarly dry conditions punctuated by very wet El Niño events, is home to most of the archipelago's endemic plant species (67 %: Porter 1979), many of which are already threatened (Tye 2008). In contrast, the smaller, wetter highland zone hosts the majority of the invasive plants in the archipelago and is already severely affected by past land-use change (Snell *et al.* 2002, Watson *et al.* 2009). Some of the potential consequences of altered seasonality are elaborated below.

Local warming and resultant increased hot-season rainfall would probably decrease soil-moisture deficits in the lowlands, thereby reducing the competitive advantage of the characteristic arid-adapted species. This effect has been observed in the short term following El Niño events, when fast-growing species thrive and grow over longer-lived species (Hamann 1985, Tye & Aldaz 1999). If conditions were permanently less extreme, the lowlands would also be more vulnerable to invasion by introduced species, which would be expected to spread from the coastal towns, where many potentially invasive species are currently cultivated in gardens (Atkinson *et al.* in press). Alternatively, if the hot seasons become drier, some species may not regenerate from soil seed banks. The importance of these seed banks to demography of some species has been suggested based on the mass germination and replenishment of their soil seed banks after El Niño rains, in places or islands where they had not been recorded before (Luong & Toro 1985, Trillmich 1991).

It is harder to say what the impacts might be in the humid highlands because changes to cool season precipitation are harder to predict, given a lack of understanding of their drivers (Sachs & Ladd 2010). It has been proposed that the cool season *garúa* has been prevalent in Galapagos for at least the last 48,000 years (Colinvaux 1972), so the biota are long adapted to this regime, so any reduction in *garúa* formation could be catastrophic for natural ecosystems. It is unclear if *garúa* would cease to form if SST were to remain above a certain level, so this is an important

Table 2. Possible effects of global climate change on Galapagos climate, by season.

| Possible changes | Hot season | Cool season |
|--------------------|--------------------------------|--|
| Trend Warmer | More convective rain, warmer. | Unknown changes to precipitation, cloud cover, humidity, wind. |
| Cooler | Less convective rain, cooler. | Unknown changes to precipitation, cloud cover, humidity, wind. |
| ENSO More frequent | More high-rainfall years. | Shorter cool seasons. |
| More intense | More years like 1983 and 1997. | More years like 1983 and 1997. |

area of future research. Changes to the hot season would likely also have impacts in this zone, although, using El Niño events as a guide, changes in productivity are not as pronounced there as in the dry zone (Hamann 1985, Luong & Toro 1985). However, one possible outcome of increased frequency of El Niño events is further damage to the highland *Scalesia* woodlands, which have already been reduced to 1.1 % of their original size on Santa Cruz (Mauchamp & Atkinson in press). This genus has suffered from mass dieback during some of the major previous El Niño events (Hamann 1985, Tye & Aldaz 1999), and impacts could be much worse now, with the increased presence of invasive plants in this community (see Mauchamp & Atkinson in press). Any such impacts would add to the already extensive degradation of the highlands.

Data needs

Despite early recognition that meteorological data were lacking for large parts of the archipelago (Alpert 1963, Hamann 1979), including the high-altitude dry zone, these data are still lacking. In particular, finer-scale data are needed, with greater spatial coverage, especially on the uninhabited islands and at higher altitudes. These would help elucidate local climate processes and their linkage with biological productivity; thereby increasing our ability to predict climate change impacts. Most of the long-term records are from coastal locations (P.R. Grant & Boag 1980), yet recent research highlights the need to understand highland processes (Bush *et al.* 2010). Some data from highland weather stations and rain gauges from S. Henderson (unpubl.), d'Ozouville (2007), Jäger *et al.* (2009) and M. Bush (unpubl.) provide interesting results but there has been no long-term monitoring. In particular Jäger *et al.* (2009) highlight the importance of interception of *garúa* by vegetation in the highland zone, paving the way for further research in that field. Also, d'Ozouville (2007) showed the importance of cool season precipitation for the recharge of the hydrological system. Satellite data may contribute to an archipelago-wide climate model, but need to be supplemented with ground-based measurements at more localities. Climate data are currently dispersed among institutions and individuals, making it challenging to collate information for an archipelago-wide understanding. When comparing rainfall data from automatic rain gauges with those from manual stations (ECCD, Bellavista, Puerto Baquerizo Moreno) and the national climate network (INAMHI), daily totals should be summed from the first time-step after 6h00 until 6h00 of the following day (see Methods, above). All data could be centralized and made available on the internet, perhaps alongside the data from ECCD and Bellavista at <www.darwinfoundation.org>. The Galapagos National Park Service could establish weather stations in more isolated sections of the archipelago, while visiting scientists with projects requiring climatic data should be encouraged to contribute data, and perhaps to

help expand a long-term climate monitoring network over the islands.

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GALAPAGOS DOES NOT SHOW RECENT WARMING BUT INCREASED SEASONALITY

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SUMMARY

Recent literature postulates that Galapagos follows global warming, with an increase in sea surface temperature (SST) and frequency and amplitude of El Niño events. However, pronounced La Niña conditions over the last decade gave rise to the question of whether the “ocean thermostat model”, according to which heating of the tropics may lead to an increase in the temperature gradient across the equatorial Pacific, enhancing upwelling and surface cooling, may better describe what has recently occurred in the Eastern Tropical Pacific (ETP). A 44-year time series of measurements of SST, air temperature and rainfall taken on the Galapagos island of Santa Cruz revealed that Galapagos monthly mean SSTs have shown no pronounced trend, while annual rainfall has increased. Mean warm and cool season temperatures have slightly increased and decreased respectively, thereby increasing seasonality. Galapagos SST data did not correlate linearly with annual rainfall, which suggests that the latter is not a reliable proxy for reconstructing past SST trajectories. When compared with those of several ETP sites, the Galapagos SST series best correlates with those of Puerto Chicama (coastal Peru, 8°S) and Cocos Island (5°N). The Puerto Chicama time series, the longest available (1925–2006), showed a negative SST trend. Annual deviations in Galapagos SST from the trend line lie between the Chicama and Cocos Island curves, and follow the El Niño signals of the Chicama series in 1983, 1987, 1992 and 1997 more closely than the Cocos series. The Humboldt Current system coupled with the El Niño Southern Oscillation may be the main driver of interannual and interdecadal changes in the Galapagos climate. Since upwelling within the Humboldt Current has increased during the last decade of extended La Niña conditions, it is no surprise that the Galapagos climate has shown the same signal.

RESUMEN

Galápagos no muestra calentamiento reciente sino aumento de la estacionalidad. Literatura reciente postula que Galápagos refleja el calentamiento global por medio de un incremento de la temperatura superficial del mar (TSM) y en la frecuencia y la amplitud de los eventos de El Niño. Sin embargo, condiciones intensas de La Niña durante la última década dieron lugar a la pregunta de si el “modelo termostático del océano” — según el cual el calentamiento de los trópicos podría llevar a un incremento de la gradiente de temperatura a lo largo del Pacífico ecuatorial, fortaleciendo el afloramiento y el enfriamiento de la superficie — podría describir mejor lo que ha ocurrido recientemente en el Pacífico Tropical del Este (PTE). Una serie de mediciones hechas a lo largo de 44 años de la TSM, la temperatura del aire y la precipitación en la Isla Santa Cruz en Galápagos revela que los promedios mensuales de la TSM de Galápagos no han mostrado ninguna tendencia pronunciada, mientras que la precipitación anual sí ha aumentado. Los promedios de temperatura de las estaciones caliente y fría han aumentado y disminuido ligeramente en forma respectiva, llevando a un incremento de la estacionalidad. Los datos de la TSM de Galápagos no se correlacionaron linealmente con la precipitación anual, lo cual sugiere que la precipitación anual no es un sucedáneo confiable para reconstruir la trayectoria de la TSM del pasado. Cuando se compara los datos de la TSM de Galápagos con otros de varios lugares del PTE, la serie de Galápagos se correlaciona mejor con las de Puerto Chicama (costa del Perú, 8°S) y la Isla del Coco (5°N). La serie de Puerto Chicama, la más extensa en disponibilidad (1925–2006), mostró una tendencia negativa de la TSM. Las desviaciones anuales de la línea de tendencia en la TSM de Galápagos se encuentran entre las curvas de Puerto Chicama y la Isla del Coco, y reflejan las manifestaciones de El Niño de la serie de Chicama en 1983, 1987, 1992 y 1997 más cercanamente que la de la Isla del Coco. El sistema de la Corriente Humboldt vinculado al El Niño Oscilación del Sur podría ser el principal motivador de los cambios interanuales e interdecadales en el clima de Galápagos. Ya que el afloramiento de la Corriente Humboldt se ha incrementado durante la última década de prolongadas condiciones de La Niña, no es sorpresa que el clima en las Galápagos esté mostrando los mismos indicios.

INTRODUCTION

In times of concern about global climate change and its impacts, the Galapagos archipelago has also become a

focal area of concern. Questions are raised about effects of temperature increase, sea level rise, changes in rainfall patterns and in El Niño frequencies and strength, on endemic species and the carrying capacity of Galapagos

(fishing pressure and tourism), when the archipelago is already impacted by El Niño. How can the human population adapt to these changes, and which are the most urgent measures to be taken?

The Galapagos climate results from a complex interplay of winds and ocean currents (Fig.1). The archipelago lies within the eastern margin of the equatorial upwelling region (EU). Nutrients are supplied to surface waters surrounding the Galapagos by equatorial upwelling and mixing and by topographic upwelling where the Equatorial Undercurrent (EUC) impinges on the western side of the islands (Chavez & Brusca 1991). EUC water is mixed both to the surface and to depth when it collides with the archipelago and eventually flows eastwards past the islands to merge with the North Equatorial Counter Current to the north and the Peruvian Undercurrent to the south (Wyrтки 1966, Kessler 2006). As a result, near-surface temperatures are lower and macronutrient concentrations higher than in the remainder of the EU or any other equatorial open-ocean region. During an El Niño warming event, winds slacken or reverse, the Intertropical Convergence Zone (ITCZ) shifts south towards the equator (Galapagos), and oceanic water from the west Pacific arrives at the archipelago, which overlays and interrupts the upwelling of cold nutrient rich waters to the euphotic layer. Sea level rises substantially and temperature on land and in the sea increase as does the amount of rainfall. The two outstandingly strong El Niño

events in 1983 and 1997 greatly affected the terrestrial and marine communities of Galapagos (Robinson & Del Pino 1985, Glynn 1988, 1994, Glynn *et al.* 2001, Jimenez 2008) and there is a general belief that these may just be the start of a series of events that will become stronger and more frequent in the coming years (Vargas *et al.* 2005).

A general consensus emerges in the scientific literature that global warming is occurring but debate continues about the order of magnitude of anticipated changes and possible regional differences. Vargas *et al.* (2005) citing McPhaden & Zhang (2002) suggested that a decrease of 25% in oceanic upwelling around the equator after 1970 may have led to an increase of 0.8°C in SST, probably reducing penguin food resources in Galapagos. Conroy *et al.* (2009) produced a calibrated sea surface temperature (SST) record at sub-decadal resolution by using diatom samples from el Junco Lake, Galapagos, and concluded that the past 50 years was the warmest period within the last 1200 years. They further suggested that their diatom index resembles Northern Hemisphere temperature reconstructions, and that recent unprecedented warming extends from the high northern latitudes, through the tropics and into the Southern hemisphere. While these and further studies (Snell & Rea 1999) suggest that Galapagos follows the global warming trend and that El Niño events are to become more frequent and greater in amplitude (Timmermann *et al.* 1999), there are other views with regard to how global warming may affect the Eastern

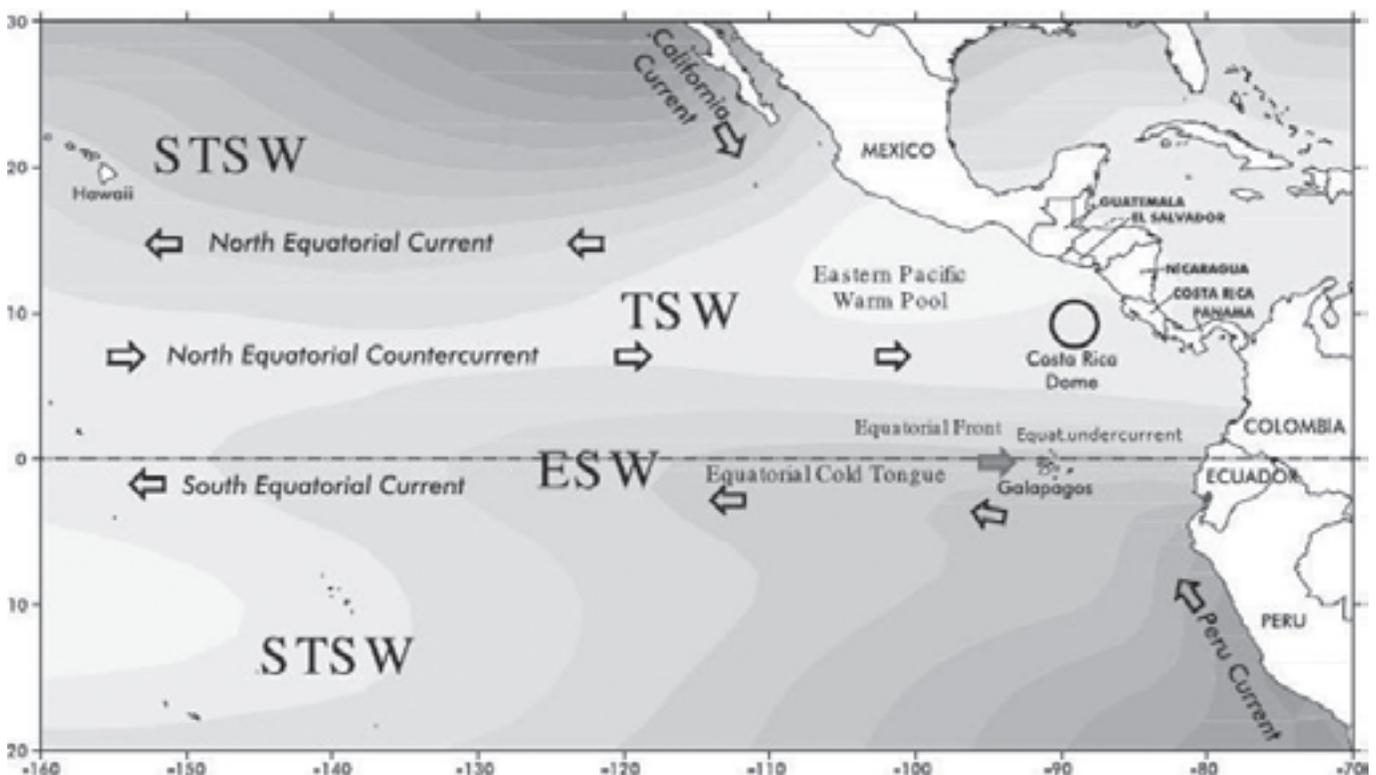


Figure 1. Surface water masses and currents in the eastern tropical Pacific Ocean. STSW = Subtropical Surface Water; TSW = Tropical Surface Water; ESW = Equatorial Surface Water. Shading represents main surface temperature: darker = colder. Adapted from Shea *et al.* (1992).

Tropical Pacific (ETP). The “ocean thermostat” model (Clement *et al.* 1996, Cane *et al.* 1997) postulates that the heating of the tropics leads to an increase in the zonal temperature gradient across the equatorial Pacific. On the eastern side, where the thermocline is shallow, cooling by upwelling opposes the surface heating. Through this increased SST gradient, wind strength and upwelling are increased and cooling occurs. In this configuration, a cold state resembling La Niña is predicted in response to warming. Vecchi *et al.* (2008) show a reconstruction of SST by Rayner *et al.* (2003), which reveals exactly this pattern: an increase in the zonal SST gradient, through robust warming in the west and weak changes (including modest cooling) in the east. Vecchi *et al.* (2008) compare several models with different temperature trajectory predictions and conclude that more observations are required to determine in which direction the Galapagos climate is moving.

The work here responds to this challenge by examining whether the generally predicted warming trend in the ETP can be confirmed for Galapagos from the data series that the Charles Darwin Research Station (CDRS) has collected over the past 44 years. An alternative hypothesis is that the Humboldt Current System (HCS) with its pronounced ENSO cycle and enhanced upwelling in recent years may affect the Galapagos climate substantially, causing mean temperatures to deviate from this general trend. Following this reasoning the Galapagos time series of SST was compared to those of several sites of the Eastern Pacific, south and north of the equator, to search for similarities in patterns and trends. The southern area of the bay of Pisco (13°30' S) was included in this analysis since it has similar emblematic species to those of Galapagos (penguins, sea lions) on small islands off Pisco and a microclimate with warmer surface waters than other parts of the central Peruvian coast. Locals sometimes call this area “small Galapagos” (pers. obs.). This region was affected as dramatically by both of the most recent strong El Niño events (1982–3 and 1997–8) as was Galapagos (Wolff & Mendo 2000, Arntz *et al.* 2006). Further sites analysed were Callao (12°S), Puerto Chicama (8°S), Esmeraldas (1°N), Gorgona (2°N), Malpelo (4°N), Cocos Island (5°N) and Panama (8°N). An additional objective of this study was to describe the trend in annual rainfall over the time period studied and to verify its correlation with SST, in order to see if rain can be used as a proxy for historical SST.

MATERIAL AND METHODS

The Galapagos data were from the CDRS meteorological station on Santa Cruz Island (0°44'20''S, 90°18'24''W). The station database contains a wide array of meteorological data since December 1964. We analyzed the series of mean air temperatures (AT) (mean of three measurements at 6h00, 12h00 and 18h00), precipitation (sum of 6h00, 12h00, 18h00) and sea surface temperature recorded with a hand held thermometer in a bucket of water pulled from the sea surface (at 6h00).

Monthly averages of SST and AT were calculated and a linear trend line for the whole data set (excluding the months following December 2007, so as to have equal proportions of data in all months January 1965 to December 2007) was computed. This analysis was repeated excluding the strong El Niño periods of the years 1983 and 1997 (*i.e.* treating El Niño years as outliers). For the SST and AT data only, the warm months Jan–Mar and the cool months Aug–Oct were also analysed separately. The moving averages for the time series of SST, AT, TP were calculated to explore periodicities in the data. Annual rainfall for the study period was calculated and correlated with annual means of SST.

Additional SST time series were used from the sites listed in the Introduction. While the Peruvian coastal SST data date back to 1950 (and in the case of Puerto Chicama to 1925) and were derived from *in situ* measurements of the Instituto del Mar del Perú, the data for the northern sites only dated from 1982 and were derived from satellite recordings (source: <http://poet.jpl.nasa.gov>). The Galapagos SST annual mean values were compared to time series from the other sites of the ETP, using linear trend lines and deviations of mean annual SST from them.

RESULTS

Analysis of Galapagos data

There was no increase in mean monthly SST over the study period (Fig. 2, $r^2 = 0.0001$). When the El Niño years 1983 and 1997 were excluded (not shown), the negative trend was more pronounced ($y = 23.5197 - 0.0007x$; $r^2 = 0.0012$). AT also showed a negative trend ($AT = 24.04 - 0.000375x$) with values about 0.47°C higher than SST. A regression of SST against AT ($SST = 0.868AT + 2.7081$, $r^2 = 0.8823$) confirms their strong correlation.

The highest SST peaks were for the strong El Niño periods 1983–4 and 1997–8. These were the only periods

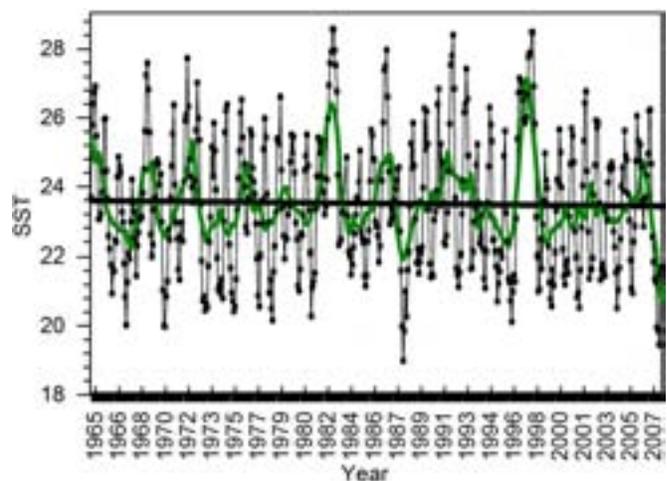


Figure 2. Monthly Sea Surface Temperature time series for Galapagos (Jan 1965 to Dec. 2007). Thick green line = 12-month moving average. Regression line: $SST = 23.57 - 0.000323x$.

for which the 12-month moving average exceeded 26°C for SST (Fig. 2). The coldest periods were in 1988–9 following the weaker 1987 El Niño and during 2007.

The mean SST during the warm season increased over the study period by 0.26°C, while during the cool season it cooled by 0.32°C (Fig. 3). This trend of increasing seasonality is confirmed by the AT data (not shown): warm season $AT = 25.996 + 0.005t$; cool season $AT = 21.785 - 0.0032t$. If the El Niño periods are excluded the same trends are seen.

During the El Niño periods 1983–4 and 1997–8, rainfall was heaviest and extended over longer seasons (Fig. 4).

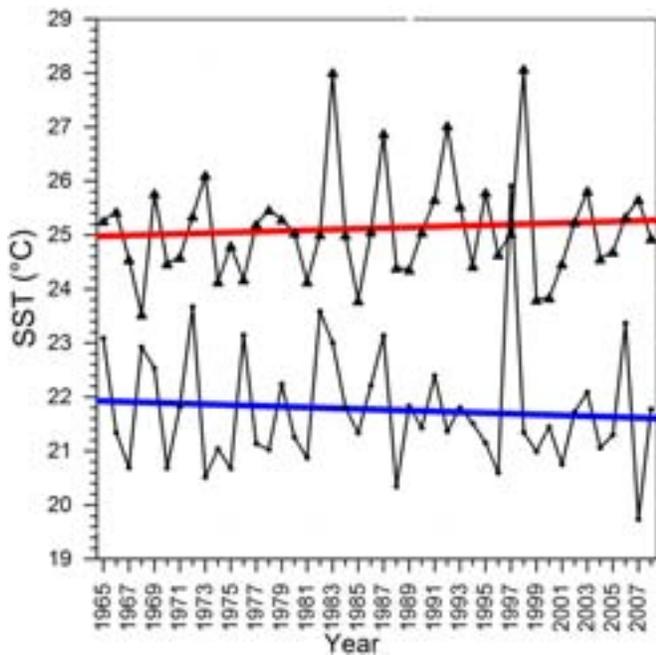


Figure 3. Galapagos mean annual SST trajectories for months Jan–Mar (upper: $y = 24.97 + 0.0067x$) and Aug–Oct (lower: $y = 21.93 - 0.0073x$).

The last decade was characterized by very low rainfall. The years 1985, 1988 and 1999, which followed El Niño periods, were almost rainless. SST and rainfall do not correlate linearly and a polynomial regression provides a better fit. It appears, however, that the correlation is absent or very weak in the SST range of 21.5–24.5°C (encircled points in Fig.4)

Comparing Galapagos with other eastern Pacific sites

The SST data series for the northern hemisphere sites was shorter (25 years) than for the southern sites (≥ 44 years). A site comparison (Fig. 5) reveals that the interannual variability in SST decreased from south to north, the Galapagos time series resembles more the southern sites than the northern with regard to the amount of inter-annual change, and the El Niño signal appears in all time series but is more pronounced in the southern sites and Galapagos.

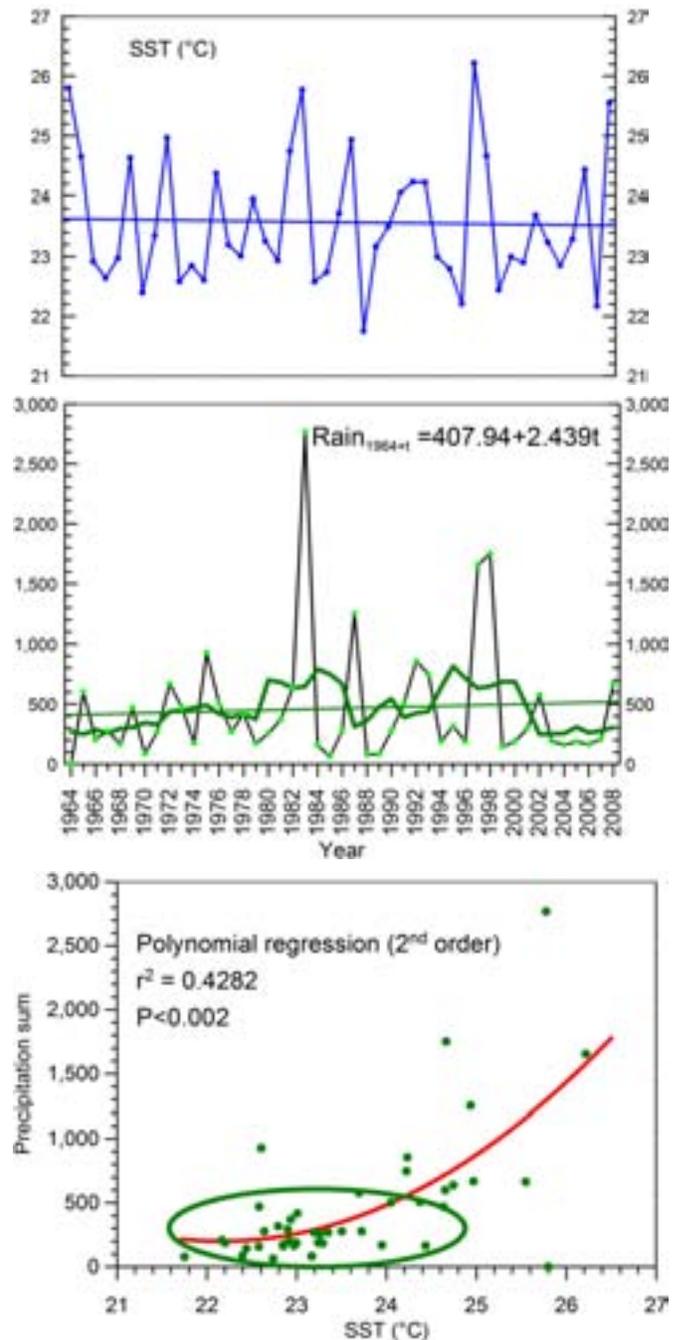


Figure 4. Galapagos time series of SST (top) and annual rainfall (middle, with linear trendline and 6-month moving average), and polynomial regression between annual rainfall (mm) and SST (bottom).

Only one site (Panama) showed a positive SST trend over the past 25 years, while Gorgona was neutral and all other sites revealed a negative trend (Table 1). The Panama time series gave the worst fit ($r^2 = 0.225$), followed by Esmeraldas and Pisco. The Cocos Island and Puerto Chicama time series correlated best with the Galapagos time series ($r^2 = 0.804$ and 0.814 respectively).

The strong, positive SST anomaly of the El Niño signals at Puerto Chicama are better matched by the Galapagos

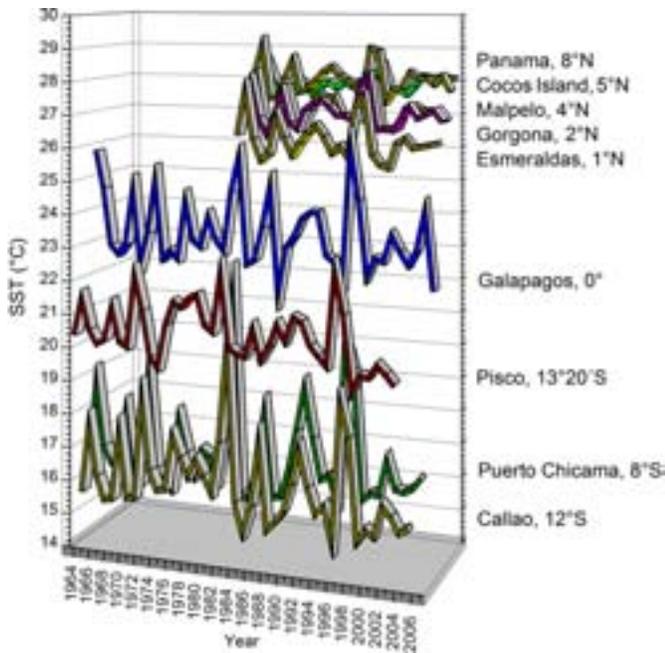


Figure 5. SST time series for sites of the Eastern Tropical Pacific.

data than the much more attenuated signal of Cocos Island (Fig. 6). On the other hand, the Cocos series is more similar to the Galapagos series outside of El Niño periods. Since the Puerto Chicama series correlated best with the Galapagos series and was the longest, the SST trend and annual deviations from the trend line were calculated for the whole 82-year period (Fig. 7). The trend was slightly negative (0.3°C decrease over the 82 years). The long time series for Puerto Chicama suggests that there was a warmer period that ended in the 1930s and which included the strong 1925 El Niño (Schweigger 1964), which was followed by a colder period lasting to the end of the 1960s. Thereafter a new warming period began, which ended with the strong 1997–8 El Niño.

DISCUSSION

The Galapagos climate data of the past 44 years do not confirm the often-mentioned global warming trend and

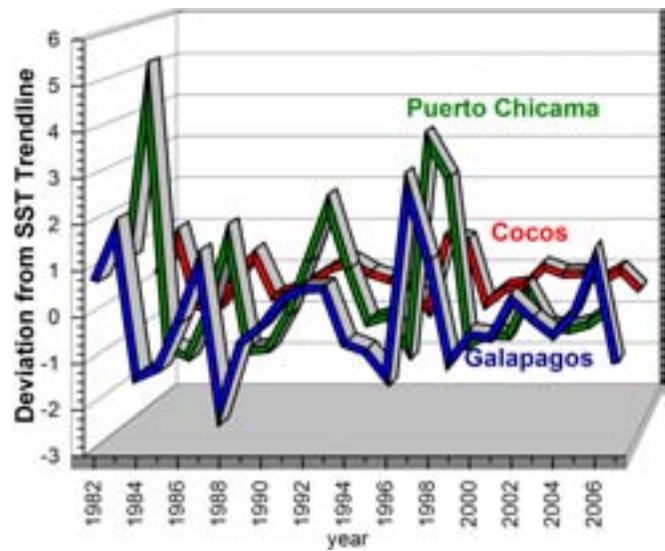


Figure 6. Annual deviations from SST trendline for Cocos Island, Galapagos and Puerto Chicama.

its expression in the ETP. Other ETP larger scale analyses based on satellite spatial averaging procedures have not considered the strong upwelling influence on Galapagos; they show a warming trend and downplay the local importance of Galapagos signals. Mean annual SST and AT have remained remarkably constant over the study period. If there is a trend at all, it is slightly negative. AT and SST correlate very well, with AT about 0.5°C higher than SST. Rainfall was strongest during the El Niño periods 1983–4 and 1997–8, when it extended over longer periods than in other years. While some rain falls in almost all years, some La Niña years following El Niño events (in 1985, 1988 and 1999) were without substantial rain. The same pattern of rainfall is known for the northern coast of Peru (Wolff *et al.* 2003). The past decade was characterized by very little rainfall and strong La Niña conditions of relatively low SST and AT.

Mean warm and cool season temperatures have increased and decreased respectively during the study period. This increase in seasonality was still seen if the two strong El Niño periods (1983 and 1997) were removed from the time series, which shows that this trend is not

Table 1. SST time series from eastern tropical Pacific sites.

| Site | Latitude | Longitude W | Data period | Temperature trend | Correlation with Galapagos (r^2) | $\Delta T^\circ\text{C}$ per decade |
|--------------|--------------|-------------|-------------|----------------------|--------------------------------------|-------------------------------------|
| Panama | 8–9°N | 79–80° | 1982–2007 | $y = 27.76 + 0.010x$ | 0.225 | +0.1 |
| Cocos Island | 5–6°N | 87–88° | 1982–2007 | $y = 28.07 - 0.001x$ | 0.804 | -0.1 |
| Malpelo | 3°50'–4°50'N | 81–82° | 1982–2007 | $y = 27.22 - 0.004x$ | 0.761 | -0.04 |
| Gorgona | 2–3°N | 78–79° | 1982–2007 | $y = 27.10 - 0.000x$ | 0.606 | 0 |
| Esmeraldas | 0–1°N | 79–80° | 1982–2007 | $y = 26.48 - 0.010x$ | 0.553 | -0.1 |
| Galapagos | 0°44'S | 90°18' | 1964–2008 | $y = 23.63 - 0.002x$ | | -0.02 |
| P. Chicama | 8°S | 79°20' | 1925–2006 | $y = 17.27 - 0.003x$ | 0.814 | -0.03 |
| Callao | 12°S | 77°15' | 1950–2005 | $y = 16.59 - 0.012x$ | 0.808 | -0.12 |
| Pisco | 13°40'S | 76°15' | 1950–2004 | $y = 20.99 - 0.007x$ | 0.550 | -0.07 |

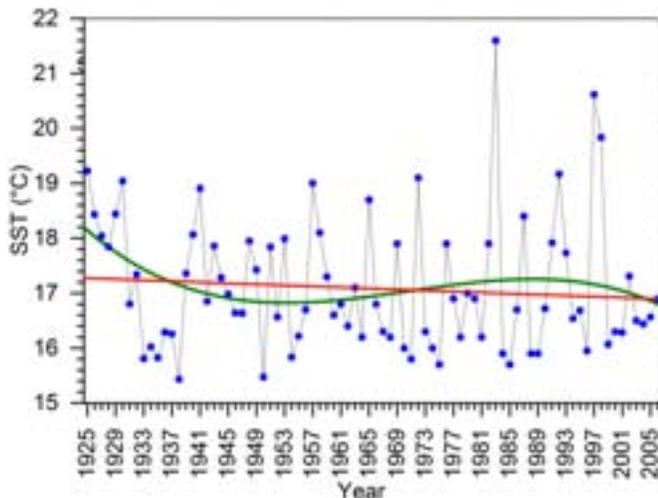


Figure 7. SST time series at Puerto Chicama, 1925–2006, with linear trendline ($SST = 17.277 - 0.0036t$) and 2nd-order polynomial.

sensitive to such outlier events. One could see this as a trend towards more temperate conditions, and it may challenge the temperature range tolerance of species such as corals. During the early cool season of March 2007, some corals died when water temperature at the 15 m isobath at Wolf Island dropped from 28°C (moderate El Niño situation) to about 16°C (La Niña situation) in six days (unpubl. data).

The SST time series revealed great similarities between Galapagos and Peruvian sites, Malpelo and Cocos Islands. The mean difference in SST between sites as distant as Galapagos and Pisco (c. 2000 km apart) was only 2.6°C (Galapagos 23.6°C, Pisco 21.0°C). Galapagos temperatures were lower than expected for most of the ETP (>25°C, Wyrski 1966), whereas Pisco temperatures were high relative to the southern upwelling centre of Peru (Wolff *et al.* 2003). The explanation for Galapagos appears to be the strong influence of upwelling, through which the otherwise tropical surface waters are cooled, whereas Pisco Bay differs from most of the Peruvian coast in being shallow and protected by a peninsula to the south, which shields it from the immediate influence of cold upwelling waters. For these reasons the Pisco area ecologically resembles the Galapagos.

The Callao site confirmed the negative trend of Galapagos and Pisco. Puerto Chicama, which lies north of Callao, was most similar to the Galapagos in SST trend, although mean temperatures were significantly lower than in Pisco Bay and more different from those of Galapagos. The 82-year time series at Puerto Chicama showed an SST decrease of 0.3°C. Since this site correlates best with the Galapagos time series, it may be speculated that a similar decrease may have occurred in Galapagos. Of all the northern sites explored, only Panama had a slight positive trend over this period, with the others following a negative trend.

Mainland coastal mean SST increased with distance from the equator (Esmeraldas 26.5°C; Gorgona 27.1°C;

Malpelo 27.2°C; Panama 27.8°C). The oceanic Cocos Island site was the warmest (28.1°C). This pattern confirms that coastal upwelling continues north of the equator, cooling the surface waters of the Ecuadorian and Colombian coasts.

Why have other authors postulated a warming trend for Galapagos over the last decades, when the observational data show that this has not happened? For example, Conroy *et al.* (2009) reconstructed Galapagos SST over the past 1200 years using a diatom proxy and concluded that the past 50 years were the warmest in that period with a tendency of continuous warming since the end of the 19th century. The explanation probably lies in the questionable concept that lake water level (which determines diatom composition) is a reliable proxy for SST. The present study shows that the correlation is rather weak and non-linear. There is a temperature range (21.5–24.5°C), where rainfall seems to be rather uncorrelated with temperature (Fig. 4), such as in 2007, when oceanographic conditions resembled La Niña but rainfall was quite strong during the warm season. However, the rainfall data used in this study may not be as spatially and temporally representative as SST, possibly introducing some noise into the analysis. Conroy *et al.* (2009) proposed that observed warming in northern latitudes extends through the tropics to the southern hemisphere, but this is contradicted by the present study, whose results rather support the “ocean thermostat model”, which predicts that wind strength and upwelling are increased through the increased SST gradient between the eastern and western side of the Pacific, and cooling occurs in the east. A cold state of the system resembling La Niña is thus predicted in response to global warming, as can be seen in the actual SST records.

The present analysis thus suggests that the Humboldt Current System with the coupled El Niño Southern Oscillation is the main driver of interannual and interdecadal changes of the Galapagos climate. Since upwelling within the Humboldt current has increased during the last decade of extended La Niña conditions, it is no surprise that the Galapagos climate has shown the same signal over the last years.

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GALAPAGOS COMMENTARY

POSSIBLE EFFECTS OF CLIMATE CHANGE ON THE POPULATIONS OF GALAPAGOS PINNIPEDS

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SUMMARY

The future of Galapagos Sea Lion *Zalophus wollebaeki* and Galapagos Fur Seal *Arctocephalus galapagoensis* populations was evaluated with reference to a conservative model of predicted climate change. Populations of both species will decrease during strong El Niño events and disease outbreaks will likely increase. Fur Seals may be exposed to a high risk of extinction if thermocline depth increases during extended warming events, since they can feed only near the surface and depend on upwelling. While predictions of the oceanographic conditions around Galapagos for the next 50 years remain uncertain, the combination of climate change and other human-induced threats (disease, disturbance, massacres and pollution) increases the need for conservation measures to protect these animals and their ecosystem.

RESUMEN

Posibles efectos del cambio climático en las poblaciones de pinnípedos de Galápagos. El futuro del Lobo marino de Galápagos *Zalophus wollebaeki* y del Lobo peletero de Galápagos *Arctocephalus galapagoensis* fue evaluado, utilizando como referencia un modelo conservativo de predicción sobre el cambio climático. Las poblaciones de ambas especies decrecerán durante eventos El Niño fuertes y posiblemente aumentarán los brotes de enfermedades. El Lobo peletero podría estar expuesto a un alto riesgo de extinción, si la profundidad de la termoclina se incrementa durante los eventos cálidos extensos, dado que estos animales sólo pueden alimentarse cerca a la superficie del océano y dependen del afloramiento. Mientras que el escenario oceanográfico de Galápagos para los siguientes 50 años encierra un alto grado de incertidumbre, la combinación del cambio climático y otras amenazas inducidas por los humanos (enfermedades, interacciones humanas, masacres y contaminación) aumenta la necesidad de medidas de conservación para proteger a estos animales y sus ecosistemas.

INTRODUCTION

The two endemic species of pinniped in the Galapagos Islands, the Galapagos Sea Lion *Zalophus wollebaeki* and the Galapagos Fur Seal *Arctocephalus galapagoensis*, are sympatric but occupy different habitats in the archipelago. Sea Lion colonies are found on sandy and rocky beaches near shallow waters all over the archipelago, whereas Fur Seal colonies occur on cliffs, near deep, cold waters. The largest Sea Lion colonies are located in the central and southern islands, whereas the Fur Seal breeding colonies are on the western and northern islands (Salazar 2002). Recent information on feeding ecology and diving behavior of the Galapagos Sea Lion revealed a wide range of use of the Galapagos Marine Reserve (GMR) waters and coastlines, and a high energetic cost of

living in these environments (Wolf & Trillmich 2007, Villegas-Amtmann *et al.* 2008, Trillmich *et al.* 2008, Kunc & Wolf 2008). The populations of both species were recently estimated to have declined by 50 % in the past three generations and both were consequently considered Endangered by criterion A2a on the IUCN 2009 red list. Climate change and the increase of introduced species were the two key threats identified. The current population of the Galapagos Sea Lion is estimated at 18,000–20,000 animals and the Galapagos Fur Seal at 8,000–10,000, based on a census in 2001 (Salazar 2002) and recent unpublished data.

Today, climate change is recognized as a major environmental problem (Pachauri & Reisinger 2007). In Galapagos the climate predictions are uncertain, but even the most conservative models (*e.g.* the IPCC-Ar4 model:

Pachauri & Reisinger 2007) predict an increase in El Niño intensity (sea surface temperature anomalies of +3 to +6°C) and La Niña events. Liu (2010) predicted a “Mega El Niño event” by 2044 and variable La Niñas in the near future. Considering the effects of the 1997–8 strong El Niño on the Sea Lion population, which caused *c.* 90 % pup mortality, *c.* 67 % alpha male mortality and a 50 % population decrease (Salazar & Bustamante 2003), Sea Lions would be severely threatened under these predicted scenarios. During the 1982–3 major El Niño event both species suffered mortality rates of 30–40 % due to lack of food (Trillmich & Limberger 1985, Trillmich & Dellinger 1991). Since both species are top predators, they play an important role in the integrity of marine and coastal ecosystems (Fariña *et al.* 2003) and are indicators of changes in their environment.

The same climate model (Pachauri & Reisinger 2007, Liu 2010, L. Xie pers. comm.) predicts high variability in precipitation and temperatures, with possible thermal shocks (abrupt changes of environmental temperatures), weakened upwelling and deepening of the thermocline. This model concords quite well with recent temperatures in Galapagos (1952–2007).

Here we examine the potential impacts of climate change on Galapagos Sea Lion and Fur Seal populations and propose management measures to improve their conservation status.

METHODS

At a workshop in 2009, an expert group addressed the likely impacts of climate change and other factors on pinniped populations in the Galapagos. Impacts were subjectively evaluated and scored as follows: no effect (0), positive effect (1 to 3), negative effect (–1 to –3) and unknown effect (?). The difference between 1, 2 and 3, positive or negative, depended on the estimated magnitude of effects with 1 as moderate, 2 as strong and 3 as very strong.

RESULTS

Previous studies show that strong El Niño events can decrease the population of Galapagos Sea Lions and Fur Seals by 50 %, and moderate events by 20 %. A very strong El Niño might cause a 60 % population loss for both species. An estimated recovery rate of 1000 Sea Lions and 500 Fur Seals per year, is based on population recovery estimates following the last El Niño events, with 20 % recovery during a moderate La Niña (2002–3), 50 % during strong La Niña (1998–9) and an assumed 60 % during extremely strong events.

Further threats such as diseases and human interactions may reduce recovery rates, and the resilience of the populations depends on conservation management. Since diseases and vectors may increase with increasing temperatures, and human impacts will likely increase with the growing human population in the Galapagos, but assuming also improved management, we set these impacts at 10 % for Sea Lions and 5 % for Fur Seals. The lower figure for Fur Seals is set since they are more isolated from such impacts than are Sea Lions. In 15 years, assuming further strong El Niño events, these impacts will decrease to 5 % and 1 % for Sea Lions and Fur Seals respectively, and in 50 years to 1 % and 0 %, because the low density of the remaining populations will reduce the likelihood of disease spread (and also assuming optimal management).

These effects are summarized in Table 1 and the impacts resulting from them are estimated in Table 2. Further strong El Niño events will severely impact both species. Some recovery will occur during La Niña events and in the following 15 years, but since continuous ocean warming may weaken future La Niñas, these benefits will be reduced as well. Deeper thermoclines and increasing water temperatures in the future will have moderate to very strong negative effects especially on Fur Seals. Further, thermal shocks have a strong impact on Sea Lions. Most of the effects associated with climate

Table 1. Population effects used for the construction of trends in Galapagos pinniped populations over the next 50 years.

| | Sea Lion | Fur Seal |
|---|------------------------|--------------|
| Estimated population size (2009) based on extrapolation from 2001 census and 2002–7 main colony surveys. | 20000 | 10000 |
| Estimated recovery rates after the last strong El Niño (1997–8). | 1000 per year | 500 per year |
| Estimated El Niño population decrease effects. | | |
| | Moderate (e.g. 2004–5) | 20 % |
| | Strong (1997–8) | 50 % |
| | Mega (assumed) | 60 % |
| Estimated La Niña population recovery effects. | | |
| | Moderate (e.g. 2005–6) | 20 % |
| | Strong (1998–9) | 50 % |
| | Mega (assumed) | 60 % |
| Other negative effects (diseases, pests, interaction with fisheries and tourism). | | |
| | Present day | 10 % |
| | +15 years | 5 %* |
| | +50 years | 1%** |

* With improved management; ** with optimal management.

Table 2. Estimates of the effects of climate change impacts on the pinniped populations in 2010, 2025 and 2060, based on the IPCC-Ar4 model (Pachauri & Reisinger 2007, Liu 2010). GSL = Galapagos Sea Lion; GFS = Galapagos Fur Seal.

| Impact | Year | GSL | GFS | Impact | Year | GSL | GFS |
|----------------------------|------|-----|-----|--|------|------------|------------|
| Strongest El Niño events | 2010 | -1 | -1 | Upwelling reduction | 2010 | 3 | 3 |
| | 2025 | -2 | -2 | | 2025 | -2 | -3 |
| | 2060 | -2 | -3 | | 2060 | -2 | -3 |
| Variable La Niña events | 2010 | 3 | 3 | Sea level increase | 2010 | 0 | 0 |
| | 2025 | 2 | 2 | | 2025 | -1 | -1 |
| | 2060 | 1 | 1 | | 2060 | -2 | -3 |
| Thermal shock | 2010 | -1 | ? | Precipitation changes | 2010 | -1 | ? |
| | 2025 | -2 | ? | | 2025 | -2 | ? |
| | 2060 | -2 | ? | | 2060 | -3 | ? |
| Ocean acidification | 2010 | ? | ? | Wind changes | 2010 | 0 | 0 |
| | 2025 | -1 | -1 | | 2025 | -1 | -1 |
| | 2060 | -2 | -2 | | 2060 | -2 | -2 |
| Deepeningthermocline | 2010 | 2 | 3 | Current changes | 2010 | 0 | 0 |
| | 2025 | -1 | -2 | | 2025 | -1 | -2 |
| | 2060 | -2 | -3 | | 2060 | -2 | -3 |
| Surge increase | 2010 | 0 | ? | Predation changes | 2010 | -1 | -1 |
| | 2025 | -1 | -1 | | 2025 | -2 | -2 |
| | 2060 | -2 | -1 | | 2060 | -1 | -1 |
| Water temperature increase | 2010 | 3 | 3 | Diseases and introduced species increase | 2010 | -1 | 0 |
| | 2025 | -1 | -2 | | 2025 | -2 | -2 |
| | 2060 | -2 | -3 | | 2060 | -3 | -3 |
| Air temperature increase | 2010 | -1 | 0 | Total | | -42 | -36 |
| | 2025 | -2 | -1 | Subtotal negative | | -56 | -51 |
| | 2060 | -2 | -2 | Subtotal positive | | 14 | 15 |
| | | | | Subtotal unknown effect | | 1 | 8 |

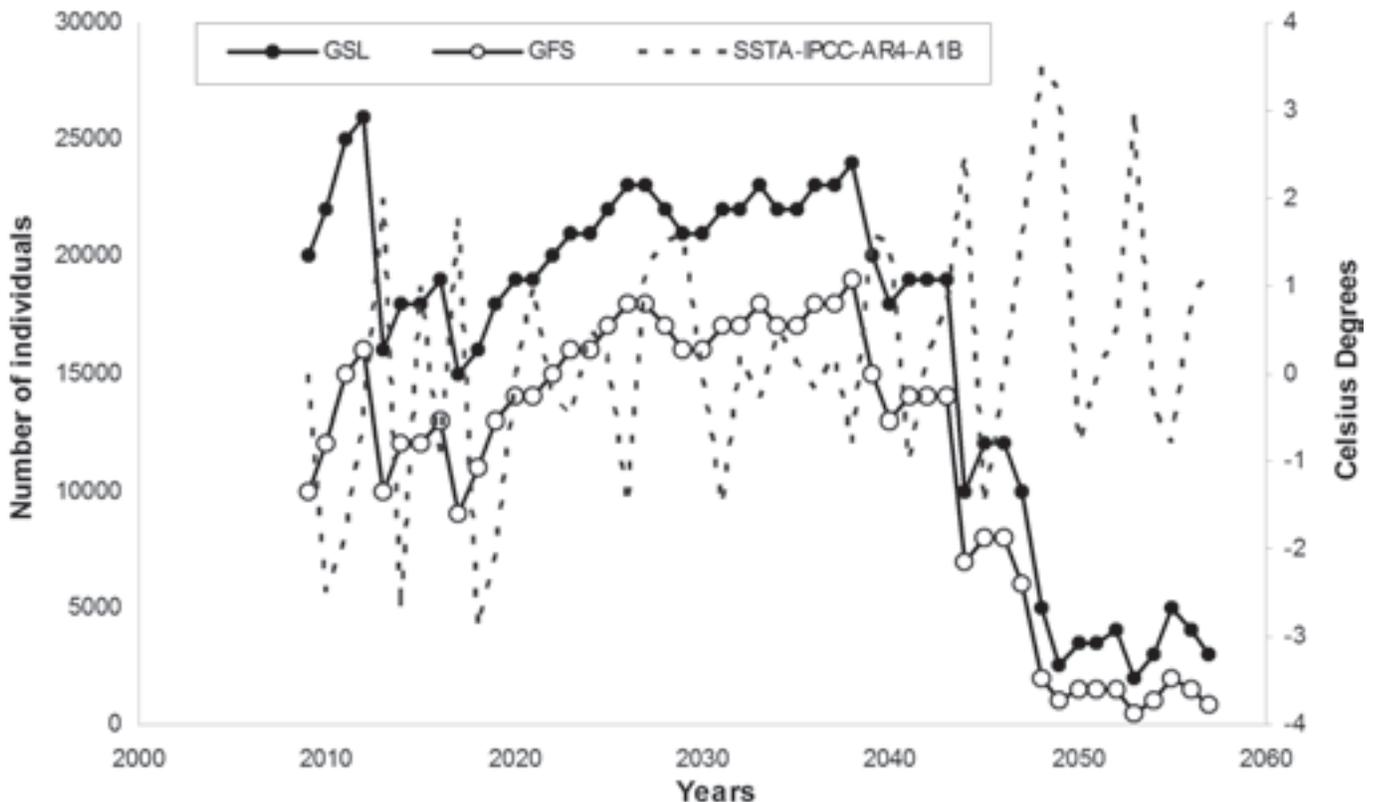


Figure 1. Possible population trends of the Galapagos Sea Lion (GSL) and the Galapagos Fur Seal (GFS) for the next 50 years in response to possible effects of climate change. The dashed line shows the predicted sea surface temperature anomalies by the model (Pachauri & Reisinger 2007, Liu 2010).

change were negative. Some, such as the effects of thermal shock and rainfall changes on Fur Seals and the consequences of ocean acidification for both species, are essentially unknown. Positive scores were mostly related to present oceanographic conditions and to La Niña effects, although the uncertainty of La Niña events in the future reduces them in the middle and long term. When all impacts are summed, the overall consequences of climate change are negative.

Using the effects estimated in Table 2 and the estimated percentages of impact of these effects, we predicted population trends for both species (Fig. 1). Both species show great population fluctuations, with reductions occurring especially during strong El Niño events. During the decade 2010–20, under presumed persistence of cold conditions, an increase to 25,000 Sea Lions and 15,000 Fur Seals seems probable. Declines could occur during weak to moderate El Niños, followed by slow recovery during the subsequent 10–15 years. Assuming weak to moderate El Niño events in 2013 and 2017, and warmer conditions from 2026 to 2029 (Liu 2010, L. Xie pers. comm.), the estimated populations in 2029 would be close to 21,000 Sea Lions and 16,000 Fur Seals. A predicted “Mega El Niño” would cause a major drop by 2040, with 60 % reduction for the Sea Lion and 70 % for the Fur Seal. Based on this model, by 2060 there might be only 3000–5000 Sea Lions and 800–1000 Fur Seals left (Fig. 1).

DISCUSSION

The population predictions outlined above were exploratory, using present population numbers, and without taking into account the high variability in dynamics between colonies which was evident during the 1997–8 El Niño, when most of the Sea Lion colonies decreased but others (*e.g.* Mosquera islet) acted as refuges, with adults increasing and *c.* 10 % of pups born at the end of 1997 surviving. Population decrease as measured in Galapagos during El Niño events includes both mortality and long distance displacement, as confirmed by more frequent sightings of Galapagos Sea Lions and Fur Seals off the continental coast of Ecuador during events (Palacios *et al.* 1997, Capella *et al.* 2001, Félix *et al.* 2007); however, our model does not take this into account. Further, the complex effects of global warming on ocean ecosystems, and the lack of data for pinniped birth and mortality rates during changing El Niño–La Niña conditions, limit prediction of trends in the populations and future consequences for these species. And so far there is little information on ecosystem effects of ocean warming and acidification, which adds uncertainty to our predictions. Over-fishing is also not addressed here and a fisheries collapse as predicted for 2048 by FAO (Worm *et al.* 2006) would dramatically affect the food sources of both Galapagos pinnipeds.

However, it is clear that the survival of Sea Lions and Fur Seals will be threatened by strong warming events.

Other threats, such as diseases, the growing human population on the Galapagos, perceived conflicts between pinnipeds and fishing activities, and pollution in colonies close by human settlements, add to these problems. Besides direct disturbance of Sea Lion colonies on populated islands, or Sea Lions being fed by fishermen in Pelican Bay on Santa Cruz, where humans or pets constantly interfere with natural behavior, they also increase the threat of infectious diseases such as canine distemper, morbillivirus and others, which are transmitted by introduced animals such as dogs, cats and rats (Salazar 2002, Alava & Salazar 2006). Since Fur Seals tend to live on isolated sites and uninhabited islands, such impacts on them are less severe, but they are more susceptible to warming events because of their diving behavior and consequent high mortality El Niño events (Trillmich & Limberger 1985, Trillmich & Dellinger 1991). For Fur Seals the changes in colony size during El Niño events are dramatic, since young animals lack the diving abilities to provide for their energy requirements (Horning & Trillmich 1997) and females cannot compensate by providing more milk during warmer conditions when prey is less available, even by exceeding their normal foraging time or depth (Trillmich 1990). An additional threat to them may be the squid fishery along the border of the GMR but its effects are as yet unknown (Merlen & Salazar 2007).

The Sea Lion’s diversity of prey and capacity to switch between feeding areas could cushion it against the effects of El Niño events and warming oceans, and there is evidence of a positive El Niño effect on genetic variation (Salazar & Bustamante 2003). However, the more specialized Fur Seal depends on upwelling close to its colonies and would have severe difficulty adapting to warming oceans. Since Fur Seals feed on vertically migrating fish and cephalopods (Dellinger & Trillmich 1999), their prey may greatly decrease as ocean temperatures increase and the thermocline deepens (Rosa *et al.* 2008). There is also evidence that ocean acidification may reduce squid abundance by reducing oxygen availability (Rosa & Seibel 2008).

Given that infectious diseases tend to increase in warmer ocean environments (Harvell *et al.* 2002), the eye fluke *Philophthalmus zallophi* and other diseases such as skin ulcers in Sea Lion pups (Merlen & Salazar 2007) present another concern; but infectious diseases in Galapagos pinnipeds need more research to determine their present and potential population impacts.

From 1995 to May 2008, naturalist guides and others reported 654 pinnipeds with signs of health problems and injuries. About 90 % of these reports refer to Galapagos Sea Lions, with intentional attack by people accounting for 54 %, including the slaughter of 53 individuals on Pinta Island in 2007. Besides, 85 % of the Sea Lion breeding colonies are used as visitor sites (Salazar 2002) and require strict management. Female Sea Lions use several resting areas other than breeding colonies (Villegas-Amtmann *et al.* 2008), which implies that management strategies

should not be limited to breeding colonies but should include the entire coastline of the GMR.

Present management decisions influence the future of Galapagos pinnipeds and their resilience to warming oceans. The workshop made the following recommendations: re-establish continuous monitoring of the colonies of both species, focusing on pup counts and five-yearly population censuses; conduct studies on the health status of pets and the risk of disease transfer between pets and sea lions; improve control of alien species such as flies, dogs, cats, rats and others that could act as vectors of disease; and educate local communities to increase respect for Sea Lions in human environments and foster their conservation especially in relation to fisheries, tourism and attacks.

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CLIMATE AND OCEANOGRAPHY OF THE GALAPAGOS IN THE 21ST CENTURY: EXPECTED CHANGES AND RESEARCH NEEDS

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SUMMARY

With the likelihood that carbon dioxide and other greenhouse-gas levels in the atmosphere will continue to increase for the next decades, and that the planet as a whole will likely warm as a result, we expect the oceanography and climate of the Galapagos to change. Based on an analysis of observational studies and climate models, the main changes are likely to include higher sea-surface temperatures, continued El Niño and La Niña events, some of which will be intense, a rise in sea level of several cm, increased precipitation, lower surface ocean pH, and a reduction in upwelling. These changes will likely alter the marine and terrestrial ecosystems of the Galapagos in ways that are difficult to predict. Major uncertainties exist concerning the relationship between the expected regional changes in ocean temperatures, precipitation, upwelling and seawater pH that most climate models consider, and the local changes in the Galapagos Islands.

RESUMEN

Clima y oceanografía de Galápagos en el siglo 21: cambios esperados y necesidades investigativas. Con la probabilidad de que los niveles de dióxido de carbono y otros gases del efecto invernadero en la atmósfera continuarán incrementándose por las próximas décadas, y de que el planeta en su totalidad seguramente se calentará como resultado, suponemos que la oceanografía y el clima de Galápagos cambiarán también. Basado en un análisis de estudios observacionales y de modelos climáticos, los mayores cambios probablemente incluirán elevación de la temperatura de la superficie del mar, continuación de los eventos de El Niño y La Niña (algunos de los cuales serán más intensos), una elevación del nivel del mar en varios cm, un incremento de la precipitación, un decremento del pH de la superficie del océano, y una reducción en las corrientes ascendentes. Estos cambios probablemente alterarán los ecosistemas marinos y terrestres de Galápagos en modos difíciles de predecir. Existen mayores incertidumbres acerca de la relación entre los cambios regionales esperados en temperaturas oceánicas, precipitación, corrientes ascendentes y pH del mar que la mayoría de los modelos climáticos consideran, y los cambios locales en las Islas Galápagos.

INTRODUCTION

In April 2009, a panel of climate scientists (listed in the Acknowledgments) convened in Puerto Ayora, Galapagos to evaluate the expected changes in the climate and oceanography of the Galapagos in the coming decades. This article represents the outcome of those discussions and may be useful to scientists and policymakers interested in the impact of future climate changes on the marine and terrestrial ecosystems of the Galapagos Islands.

TEMPERATURE CHANGE

As of 2007, there had been no discernible trend in sea surface temperature (SST) in the region of the Galapagos ($2^{\circ} \times 2^{\circ}$, or about 200×200 km, centered on 0°N , 90°W) since the start of the Industrial Revolution (Smith *et al.* 2008). Nor was there any trend in local SSTs at Santa Cruz Island in the Galapagos over the last 44 years (Wolff 2010). Yet the larger equatorial Pacific, as indicated by the Niño 3 index of SST in the region $90\text{--}150^{\circ}\text{W}$ and $5^{\circ}\text{S}\text{--}5^{\circ}\text{N}$,

has warmed by $0.4\text{--}0.8^{\circ}\text{C}$ over the last 40 years, and warming throughout the region is expected to continue over the course of the 21st century, with the best estimates indicating $1\text{--}3^{\circ}\text{C}$ of additional warming (IPCC 2007a). Whether local SSTs in the Galapagos will continue to buck the warming trend observed in the greater equatorial Pacific region over the last 40 years is unknown. But it seems imprudent to extrapolate from a failure to follow the regional temperature trend when that trend is only $0.4\text{--}0.8^{\circ}\text{C}$, and conclude that local SSTs will not rise in the face of the expected $1\text{--}3^{\circ}\text{C}$ of warming in the equatorial Pacific region this century.

Additionally, despite the overall trend towards warmer SST in the equatorial Pacific, decadal variability will likely continue, but this variability may well be stochastic, and there is a large consensus that its spectral character approximates a red noise process, with more power at lower frequencies (Gedalof *et al.* 2002). In other words, predicted decadal variability in equatorial Pacific SST can best be described as predominantly random with some memory. One of the most prominent decadal

variations, the Pacific Decadal Oscillation, may not force temperature changes, but could simply result from the El Niño-Southern Oscillation (ENSO) (Newman *et al.* 2003).

A lack of understanding of the linkage of large-scale analyses (*e.g.* IPCC-type) to local scales as in Galapagos remains, and this knowledge gap should be a focus for future research. There is a clear need for more meteorological and hydrographic observations, combined with widespread data dissemination, so existing time series of SST and meteorological conditions can be compared. One step towards achieving this aim would be to reinstate the rawsonde program in the Galapagos, which made daily weather balloon deployments to measure atmospheric temperature, pressure, humidity, wind speed and wind direction through the atmosphere above San Cristóbal Island from 1990–8. Additional research should focus on down-scaling models, especially atmospheric ones, by including more ensemble members (*i.e.* numerical predictions using slightly different initial conditions), with assistance from ocean dynamics researchers. Paleoclimate records can also be used to link large-scale analyses to local scales. Future research should focus on generating new paleoclimate records, especially from the lowlands, and linking them to more recent instrumental records. Calibration of paleoclimate proxies under modern conditions should be an integral part of this. Finally, we need a better understanding of the dynamics and interactions of the Panama and Humboldt Currents with the Galapagos (see below).

EL NIÑO SOUTHERN OSCILLATION

The ENSO is the dominant inter-annual global climate variable that strongly impacts the Galapagos (Cane 2005, Philander 1983). During El Niño events, the surface ocean around the Galapagos warms substantially and the islands receive significantly more rainfall than in normal years. The warmer water is poorer in nutrients than the cool waters that normally surround the Galapagos, which disrupts the marine ecosystem, causing mass mortality of coral, seabirds and marine mammals during the strongest events, such as those in 1982–3 and 1997–8 (Glynn 1988). Major changes to terrestrial ecosystems also occur, with heavy rain permitting the establishment of newly colonizing plants and animals, and dramatic increases in the biomass of herbaceous plants and vines at the expense of cacti (Hamann 1985, Luong & Toro 1985, Tye & Aldaz 1999, Holmgren *et al.* 2001).

Since 1880 A.D., ENSO events have occurred roughly every 2–7 years, with no clear periodicity (Cane 2005). The late 20th century was characterized by particularly strong and frequent events that led some researchers to conclude that an anomalous and unusual change had occurred in ENSO that could be attributed to increased levels of atmospheric greenhouse gases (IPCC 2001, IPCC 2007B, Trenberth & Hoar 1997). This claim has been challenged by other researchers and at best it is uncertain

(Cane 2005, Rajagopalan *et al.* 1997). The duration of the instrumental record of SST and atmospheric pressure is too short to conclude that a fundamental change in ENSO variability has occurred (Wunsch 1999). Though supported by some theory and models (Timmermann *et al.* 1999), a link between greenhouse-gas-induced global warming and increased frequency or intensity of ENSO events remains inconclusive (Collins 2000), with the average of projections from coupled ocean-atmosphere general circulation models showing no change in ENSO variability over the 21st century (Collins & Groups 2005, IPCC 2007a), but rather a tendency toward a more El Niño-like state of the tropical Pacific (Cane 2005). In all likelihood, ENSO-related variability will continue in the coming decades and is likely to modulate SST, rainfall and sea level changes in the Galapagos on inter-annual timescales (IPCC 2007a).

Future research in this area should include continued efforts to understand the long-term behavior of ENSO; this is a major research thrust by IPCC-related researchers and modelers. Additionally, it is necessary to develop ENSO indicators relevant to local conditions. For example, 2008 was characterized by high rainfall in the Galapagos even though it was not an El Niño year.

SEA LEVEL RISE

Global mean sea level has risen by *c.* 20 cm since 1880 A.D. as a result of global warming and the rate of increase has accelerated since about 1930 (IPCC 2007a). However, the rate of sea level rise since the mid-20th century has not been as significant in the eastern equatorial Pacific as in other parts of the world (IPCC 2007B). There has been no discernible trend in sea level over the last 26 years on Santa Cruz Island in the Galapagos (Fig. 1). Nevertheless,

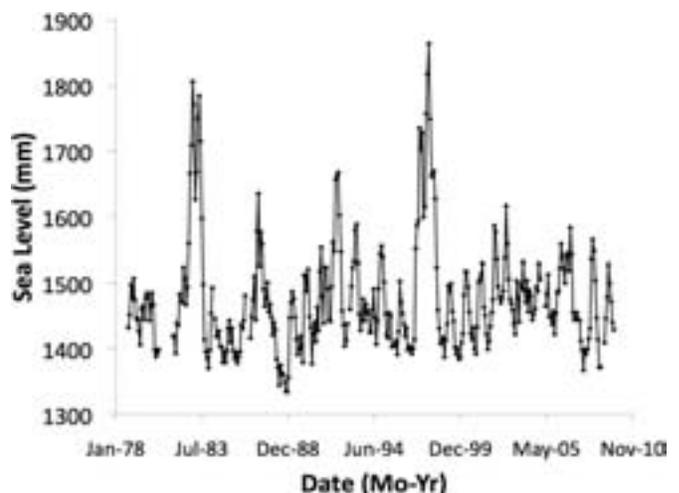


Figure 1. Sea level at Santa Cruz, 1982–2008. No significant trend exists. The two large El Niño events of 1982–3 and 1997–8 are visible as periods of higher than normal sea level. Data from the University of Hawaii Sea Level Center <<http://uhslc.soest.hawaii.edu/>>.

global mean sea level is projected to rise by 20–50 cm (IPCC 2007a) or more (Rahmstorf *et al.* 2007, Solomon *et al.* 2009) over the 21st century. In the Galapagos, subsidence of some of the islands, or portions of them, has the potential to exacerbate local sea level rise in the coming decades.

Adaptation to sea level changes may be viewed through the lens of strong El Niño events, which cause sea level in the Galapagos to increase by up to 45 cm, as occurred during the 1997–8 event (Fig. 1). Recent land use changes (*e.g.* coastal development) have made the Galapagos much more vulnerable to even modest rises in sea level, including those associated with El Niño (Clarke & Van Gorder 1994, Clarke & Lebedev 1999). It is important to determine why local sea level in the Galapagos has not been observed to rise in concert with the modest rise in sea level in the eastern equatorial Pacific, and to monitor local rates of subsidence, which may exacerbate the rise in global sea level. It would therefore be advantageous to augment the tide gauge on Santa Cruz with additional gauges throughout the archipelago.

PRECIPITATION

Mean annual precipitation in Puerto Ayora, Santa Cruz Island, has varied significantly over the last 45 years, with El Niño years being characterized by high rainfall and La Niña years characterized by low rainfall (Trueman & d'Ozouville 2010). But this relationship can break down, as observed in 2008, a non-El Niño year, when rainfall amounts were greater than in several El Niño years of the last half century. On longer time scales, rainfall reconstruction from the sediments of El Junco crater lake on San Cristóbal Island indicate that the Galapagos have been trending toward a wetter mean climate in the past 130 years (Sachs *et al.* 2009). The driest period of the last 1200 years in the Galapagos was apparently the end of the 19th century, which we attribute to the end of the northern hemisphere climate anomaly known as the “Little Ice Age” (Grove 1988). Since that time there has been a trend toward wetter conditions, though even modern rainfall amounts are lower than any other time in the last 1200 years prior to about 1880 AD. Reconciling our sediment data, which indicate increasing precipitation over the last several decades, with the observations for the last 45 years which indicate no significant trend in precipitation (Wolff 2010), is possible considering that the El Junco sediment samples average over *c.* 30 years of deposition, and there could also be differences in rainfall recorded at sea level on Santa Cruz Island and at 750 m on San Cristobal Island. Nevertheless, if the century-long trend toward a wetter climate in the Galapagos that is implied by the El Junco data continues, we would expect the Galapagos to receive increasing rainfall in the coming decades.

Whether the trend toward increased precipitation since the start of the Industrial Revolution is connected to anthropogenic alteration of the climate is unknown,

but the IPCC indicates a > 90 % chance of increased precipitation over the 21st century in the region of the Galapagos (IPCC 2007a). As discussed for temperature, local changes will not necessarily follow regional changes, and a critical downscaling question concerns the trend of local Galapagos rainfall in the future. Much more extensive measurement of Galapagos weather (in both the highlands and the lowlands) needs to occur in order to address this question.

In addition to overall precipitation trends, it is necessary to assess the impact of a warming global climate on *garúa*, the mist that forms from low stratus clouds, typically during the cool, dry season lasting from June to December. This water source is critical to highland plants and ecosystems. Future trends in *garúa* formation, duration and elevation are uncertain because its formation depends on a complex interaction of SST, wind and humidity. We surmise, however, that a weakening of the Walker circulation, as predicted by theory and many global circulation models (GCMs) (DiNezio *et al.* 2009, Vecchi & Soden 2007, Vecchi *et al.* 2006), would likely result in a reduction of *garúa* in the Galapagos. In addition, if local SSTs increase, especially in the cool, dry season, the optical depth (the proportion of light absorbed or scattered by fog) and/or the seasonal duration of *garúa* would be expected to decrease. On the other hand, if the frequency and/or intensity of La Niña events were to increase, or there were an increase in local upwelling, the reverse might ensue.

Another complication is that although it is tempting to use past ENSO events as a model for the influence of a warmer ocean on precipitation in the Galapagos, ENSO may not be a good model for long-term climate change. The existence of a spatial pattern of SST in the tropical Pacific which is similar to that during an El Niño event does not necessarily imply that the underlying dynamics are the same (DiNezio *et al.* 2009, Vecchi & Wittenberg 2010).

Future studies should focus on understanding the dynamics of *garúa* formation, including establishing whether there is a threshold SST above which *garúa* will not form, and what the influence of the large-scale ocean-atmosphere circulation is on *garúa* formation. Better understanding of *garúa* formation might be achieved by analyzing existing precipitation, SST, humidity (both highland and lowland), pressure and wind data to determine the conditions under which *garúa* forms and persists.

OCEAN ACIDIFICATION

An increase in atmospheric carbon dioxide levels from 290 to 385 ppm since the start of the Industrial Revolution has caused the global ocean pH to decline by 0.1 since 1880 A.D. and an additional 0.4 pH unit decline is expected by the end of this century (Caldeira & Wickett 2003). The increased acidity of seawater will make the production

of calcium carbonate shells by marine plants and animals increasingly difficult (Orr *et al.* 2005). Making matters worse, regions where upwelling produces surface water already rich in CO₂, such as the Galapagos, are more sensitive to increases in CO₂ (Doney *et al.* 2009, Manzello *et al.* 2008). This is demonstrated by the high buffer (Revelle) factor in the region of the Galapagos relative to most of the tropical and subtropical ocean, which indicates a decreased ability to counteract pH changes when atmospheric CO₂ concentration increases (Sabine *et al.* 2004).

The upshot is that calcifying organisms and the marine ecosystem in the Galapagos are likely to be more sensitive to an acidifying ocean than the rest of the globe, as atmospheric CO₂ levels rise. When atmospheric CO₂ levels reach 450 ppm, which will likely occur by mid-century, coral growth is predicted to be at *c.* 50% of its pre-industrial rate (Silverman *et al.* 2009), due to a combination of higher SSTs and lower aragonite saturation levels (Fabry *et al.* 2008, Feely *et al.* 2008, Hoegh-Guldberg *et al.* 2007, Silverman *et al.* 2009). Coral reefs in the Galapagos will likely become incapable of surviving if atmospheric CO₂ levels reach 750 ppm (Silverman *et al.* 2009), the level expected by the end of the 21st century (IPCC 2007a).

Future study should address the relative vulnerability of Galapagos coral to ocean acidification, given that these corals already experience large swings in pH associated with ENSO.

UPWELLING

Many of the most sophisticated coupled ocean-atmosphere GCMs predict a reduction in trade wind strength, the Walker Circulation, surface currents, and vertical ocean velocity in the equatorial Pacific as a whole, but to a lesser extent in the eastern equatorial Pacific, as atmospheric CO₂ levels rise (DiNezio *et al.* 2009, Vecchi & Soden 2007). Weaker trade winds and equatorial surface currents are expected to reduce upwelling, Ekman divergence (the movement of water to the north and south of the equator caused by easterly winds at the ocean surface), and the east-west thermocline tilt (DiNezio *et al.* 2009).

Unfortunately, it is difficult to discern what the changes in upwelling in the Galapagos will be. This local upwelling results from a complex interplay between the bathymetry, the South Equatorial Current that flows west at the surface, and the Equatorial Undercurrent that flows east in the subsurface (Eden & Timmermann 2004). The Archipelago presents a topographic barrier that disrupts the flow of these major currents and tropical instability waves, such as the Kelvin waves that are generated during El Niño and La Niña events (Eden & Timmermann 2004). The Galapagos are small when compared to the scale of most general circulation models, and the processes that cause upwelling to occur there are influenced by basin-wide features as well as small scale bathymetry, so it is not yet possible to predict how changes in the ocean-atmosphere circulation will affect Galapagos upwelling.

The same downscaling issues exist as discussed for temperature and precipitation.

The Panama and Humboldt Currents also affect the Galapagos, but there are too few model studies to predict how these currents are likely to change during the present century. Such studies should be included in future research.

CONCLUSIONS

Over the next several decades, the Galapagos will experience changes related to global warming. Although varying degrees of uncertainty exist for each factor, the future of the Galapagos will most likely include continued ENSO events, some of which may be intense, increases in sea level, precipitation and surface ocean temperatures and acidity. However, many uncertainties and areas for research remain, particularly concerning the relationship between local and regional SSTs, precipitation, upwelling and acidification.

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FORTY YEARS OF PALEOECOLOGY IN THE GALAPAGOS

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SUMMARY

The Galapagos Islands provided one of the first lowland paleoecological records from the Neotropics. Since the first cores were raised from the islands in 1966, there has been a substantial increase in knowledge of past systems, and development of the science of paleoclimatology. The study of fossil pollen, diatoms, corals and compound-specific isotopes on the Galapagos has contributed to the maturation of this discipline. As research has moved from questions about ice-age conditions and mean states of the Holocene to past frequency of El Niño Southern Oscillation, the resolution of fossil records has shifted from millennial to sub-decadal. Understanding the vulnerability of the Galapagos to climate change will be enhanced by knowledge of past climate change and responses in the islands.

RESUMEN

Cuarenta años de paleoecología en las Galápagos. Las Islas Galápagos proporcionaron uno de los primeros registros paleoecológicos de tierras bajas en los Neotrópicos. Desde que las primeras muestras sedimentarias fueron levantadas en las islas en 1966, ha habido un incremento sustancial en el conocimiento de los sistemas del pasado, y en el desarrollo de la ciencia de paleoclimatología. El estudio en las Galápagos de los fósiles de polen, diatomeas y corales, y de los isótopos de componentes específicos ha contribuido a la maduración de esta disciplina. A medida que la investigación ha trascendido desde las preguntas sobre condiciones en la era glacial y estados promedio del Holoceno, hacia la frecuencia pasada de El Niño Oscilación del Sur, la resolución de los registros fósiles se ha refinado desde milenial a sub-decadal. La comprensión de la vulnerabilidad de las Galápagos al cambio climático mejorará con el conocimiento de pasados cambios y respuestas climáticos en las islas.

INTRODUCTION

The Galapagos Islands are iconic for their isolation and their place in the development of evolutionary theory. As understanding of evolutionary processes on the islands has grown, so too has the realization that both long- and short-term habitat changes may influence niche (Grant & Grant 1985). For such small islands, the breadth of terrestrial habitats on the Galapagos is impressive, from lowland semi-desert to humid montane. Each of these habitats offers challenges and opportunities for invading species, be they natural invasions over millions of years, or those induced by the human activity of the last 200 years. For each habitat, climate change can alter the balance of which species can establish a population or win in competition: dry times may relatively favor the invasion of the uplands, whereas wet times allow access to the lowlands. Consequently, understanding the scope of habitat change induced by past climate change is an important part of understanding the evolutionary history of these islands and predicting what may lie ahead.

The islands lie in the heart of the warm tongue of water that characterizes many El Niño events in the eastern equatorial Pacific and, as such, are highly sensitive to changes in ocean and atmospheric circulation. Much of the modern paleoclimatic interest in the islands relates to testing predictive models of climate, but this was not what drove the first paleoecological research on the islands. In this retrospective, we provide a historical context for the maturation of ideas relating to the paleoecology and paleoclimatology of the islands and also how the islands have played a role in the development of these disciplines. We conclude by considering how that role will continue as we seek to predict the impact of future climate changes.

THE EXPLORATORY PHASE

In 1966, Colinvaux (1968) conducted the first paleoecological reconnaissance of the Galapagos Islands. He reported on fourteen lakes, most of which were saline or hypersaline lagoons. The only permanent freshwater lake

on the islands was El Junco crater lake, San Cristóbal. Colinvaux's expedition came at a time when the first reports of ice-age tropical cooling were emerging. A long palynological record from the high plains of Colombia depicted multiple glacial-interglacial cycles manifested by the replacement of Andean forest (interglacial) with paramo (glacial) (Van der Hammen & González 1960). Meanwhile, research was also taking place in the highlands of Costa Rica (Martin 1964). In both settings, cooling appeared to be the dominant signal of the ice age, but effects on the lowland Neotropics were virtually unknown. That the tropics became much drier as they cooled was a logical extension for European researchers familiar with transitions from boreal to steppe environments (Godwin 1956). But although Colinvaux's intent was to answer the fundamental ecological question of why there are so many species in the tropics compared with high latitudes, climate history was to be important in his quest. That Colinvaux started this research in the Galapagos rather than in the Amazon, was part serendipity and part pragmatism: surely a simple flora would be easier to learn than a complex one.

Colinvaux recovered a 16-m sediment core from El Junco with a basal age beyond the limit of bulk radiocarbon dating (effectively 35,000–38,000 years). Fossil pollen and spores were well preserved in the Holocene (defined as the last 11,000 years) sediments (the upper 3.3 m of the core), and revealed a largely constant floral history for the past 12,000 years (Colinvaux 1972, Colinvaux & Schofield 1976a, b). Given the isolation of the islands, it is implausible that large-scale migration from the mainland occurred, even with glacial cycles. Furthermore, given that almost all species on the islands did not evolve *de novo* in the last 36,000 years, all floral responses to climate change would have comprised a reshuffling (or loss) of existing species. Beneath the organic Holocene sediments lay 12 m of red clays. No pollen or spores survived in those clays and their low organic content pointed to severe oxidation. In other words, during the last glacial maximum (c. 26,000–22,000 years ago) and the subsequent de-glacial period (c. 22,000–13,000 years ago) the lake was dry. The inference was clear, less precipitation would cause the lake level to drop, allowing the sediments to oxidize (we will return to this idea later). However, within that thick clay band lay a lens of organic-rich lake mud that yielded radio-carbon ages >36,000 years. In that mud, the pollen assemblage was similar to that of the Holocene section, but this earlier lake had supported a different species of *Azolla* than that in the Holocene, as well as *Myriophyllum*, a genus no longer found on the islands (Schofield & Colinvaux 1969). The period of low lake level appeared to have caused the local extinction of these aquatic species.

Colinvaux (1972) hypothesized that the cause of the drying was the northward migration of the annual range of the ITCZ, such that its southern boundary lay permanently to the north of the Galapagos. The ITCZ is a region of strong convection where the trade winds

converge. During a year, the ITCZ migrates, tracking the warmest ocean water across the Atlantic and Pacific Oceans. The arrival of the ITCZ heralds the onset of the wet season, and should it fail to reach a given location, rainfall for the year may be greatly reduced. Newell (1973), a climatologist, responded to Colinvaux's suggestion by observing that steepened temperature gradients between the vast Laurentide ice-mass and the equator would have made a northward ITCZ migration far less likely than a southerly one, and subsequent research provides overwhelming support for the ITCZ migrating southward of its modern position during cold episodes (Haug *et al.* 2001, Chiang *et al.* 2003, Sachs *et al.* 2009). Thus the discussion of the placement of the ITCZ in the Eastern Equatorial Pacific during glacial-interglacial cycles began in the Galapagos.

Johnson & Raven (1973) highlighted the potential importance of the drying of the Galapagos highlands in explaining the unusual relationship of endemic species to elevation on the islands. On most oceanic islands endemism increases with elevation, but the opposite is true on the Galapagos. If the islands lost their cloud cover, arid zone species would have moved upslope and displaced the montane elements, so the montane flora may be essentially a product of the Holocene (Johnson & Raven 1973).

Another target of the exploratory research phase was the hypersaline landlocked crater Lago Guerrero of Genovesa. The lake is about 29 m deep, and is apparently connected to the ocean by subterranean systems. The low rainfall of Galapagos precludes the maintenance of lowland lakes without hydrological subsidy from the ocean. Because of strong evaporation, these lakes become hypersaline. L. Guerrero even has a tidal cycle, but because of the complex phreatic pipes and sumps connecting it to the ocean, that cycle is a few hours out of phase with adjacent Darwin Bay. The 6-m core raised from the deepest part of the lake was beautifully banded, with hundreds of fine laminations separated by plates of white carbonate. A crucial question was: how can a lake in what appears to be a very stable setting develop banded sediment?

At high latitudes, annual bands in lakes often occur as a couplet, or pair of bands, formed by spring thaw and summer algal blooms. When such annual structure is found, it guarantees that there has been no post-depositional bioturbation, and allows researchers to reconstruct records at annual, even seasonal, scales. In the tropics, banded sediments usually reflect storm events, or the onset of rainy season conditions that erode weathered clays to form a reddish layer, followed by an algal bloom that forms a green or black layer (Bush *et al.* 1992). These banding events are seldom truly annual. Another means of forming laminated sediments is if the lake is fluctuating between supersaturated and fresher states. Each time that evaporation drives lake level down, salts precipitate to form a layer of gypsum or calcium carbonate, which appears as a thin white band. As the lake becomes fresher, algal material is deposited as a contrasting layer. Again,

these laminations are unlikely to be truly annual. In his original sedimentary description of the islands, Colinvaux (1968) alluded to such mechanisms to explain the changes in sediment color in the mid-Holocene core section from El Junco, but the exact origin of the laminations remained obscure.

Both the Genovesa record and the El Junco record contain sections of core that are finely laminated. In the case of El Junco, the banding probably reflects changes in the precipitation:evaporation balance, leading to deep conditions with hypoxic bottom water and very little bioturbation. The laminations of the lowland lakes, however, cannot be explained so simply. These lakes do not have catchments of weathered clay, and so long as sea-level is stable their level is basically invariant with respect to climate because of direct connection with the ocean. Consequently, the sediments should be monotonous in color, chemistry and texture; but they are not. The Genovesa sediments are very complex, but a strong discontinuity in the core is evident at about 2 m depth. Deep rust-reds alternate with ochre-colored sediments in the upper 2 m section, whereas blue-green layers alternate with dull emerald green layers and black sections lower in the core. In this case, the white bands do not appear to have been derived under evaporitic conditions; at least some of them are composed of almost pure layers of coccolithophores (single-celled marine algae with platy exteriors of CaCO_3). Other white bands are comprised of calcium carbonate crystals, and one grayish-white band appears to be a tephra. Textures of the bands vary from being almost gelatinous to being as brittle as thin china. How can such an apparently constant sedimentary context produce such complex patterns?

An early hypothesis was that some of the pattern may have been biologically induced through variations in the size of sea-bird colonies (Goodman 1972). Genovesa supports about 250,000 boobies *Sula* spp., which can move substantial amounts of marine-derived nutrients, particularly phosphate, onto the island. If variations in booby colony size changed through time, so too would the phosphate loading of the lake, and the algal biomass of the sediments. The Genovesa core proved undatable with conventional large-sample radiocarbon techniques, as sections of the upper 2 m of the column had ^{14}C ages older than those below. The unruly dates, which all ranged between 4400 and 6400 years in age, prevented a full analysis being published (see Goodman 1972).

In 1969, a novel hypothesis of climate change that projected vast Amazonian droughts during the ice ages, grabbed the attention of paleoecological researchers (Haffer 1969). The Galapagos were taken as a prime example of this aridity, as proponents and detractors of the "refuge hypothesis" sought to test the antiquity of Amazonia as a primarily forested biome. Perhaps because the paleoecological answer for the Galapagos was "known", and the obvious coring sites had been exploited, the islands were largely ignored for several decades.

TRANSITION TO HIGH-RESOLUTION SAMPLING

Paleoecological data from the Amazon and adjacent regions pummeled the refugial hypothesis (Colinvaux 1987, Bush & Colinvaux 1990, Colinvaux *et al.* 2001) and demonstrated that there had been no such widespread long-lasting aridity. There had been drought-prone episodes in the last 2 million years, but not ones that lasted for the 100,000 years of recent ice ages. Rather they seemed generally to last < 10,000 years, and to be too weak to disrupt the Amazon forest landscape (Bush *et al.* 2002). The explanation was that tropical lowland climates were influenced by the precession of the equinoxes, which causes the Earth's axis of tilt to point closer to or further from the sun at midsummer's day. This either enhances seasonality (pole points towards the sun in hot, wet season) or depresses it (pole points away from the sun in hot, wet season). An entire precession cycle takes 19,000–23,000 years to complete and results in dry events that last less than half a cycle. Based on precession, a mid-Holocene drought would be predicted for the southern Neotropics.

In South America, such a dry event was first documented in the Andes, by Servant *et al.* (1981), but was largely ignored because researchers were still focused on the glacial period. However, as records from Amazonia and the Andes accumulated, it became clear that a low lake stand between *c.* 9000 and 4000 yr BP in the southern hemisphere coincided with a time of high lake level in Central America and the Caribbean (Hodell *et al.* 1991, Bush *et al.* 1992, Baker *et al.* 2001, Bush *et al.* 2007). The Galapagos, sitting on the equator, showed evidence of moderate drying at this time, but not the extreme conditions of the Altiplano. The data from the initial investigation of El Junco had revealed a dry basin throughout the last glacial maximum and into the Holocene, but the dry event that Colinvaux & Schofield (1976a, b) documented between 9000 and 5000 BP did not repeat the full loss of the lake, and so was evidently not as severe.

Until the 1990s, most paleoclimatologists had thought of the glacial and the various climatic convulsions associated with de-glaciation in the North Atlantic region to be more interesting and dynamic than the Holocene. Arguably, we had tried to understand the past without fully understanding the variability of the present. Although wreaking havoc in the marine fauna of the Galapagos (Robinson 1985) and inducing exceptional productivity in terrestrial systems (Grant & Grant 1985), the importance of the El Niño event of 1982–3 was not immediately recognized by most paleoecologists. As the global significance of these events became apparent, attention was turned on the eastern equatorial Pacific, but this time the resolution of the studies had to be at the scale of the El Niño Southern Oscillation (ENSO) rather than the millennial oscillations of glaciation.

Historical records provided some basis for evaluating changes in El Niño frequency since the 1500s (Quinn *et al.* 1987). However, as Ortlieb (2000) pointed out, some of

those records could easily be misinterpreted. Ecuador's Quelccaya ice-cap provided one of the first longer records of El Niño activity (Thompson *et al.* 1986), but this only extended the record back to about AD 500.

Because the Galapagos lay in the heart of the eastern equatorial Pacific it became an obvious place to look for the long-term history of El Niño. Almost certainly, the banded sediments from Genovesa held a clue to ENSO history, but the problems associated with dating them forced researchers to look elsewhere. A new 4-m core was raised from the crater lake on Bainbridge Rocks, which was dated using ^{14}C accelerator mass spectrometry (Steinitz-Kannan *et al.* 1998, Riedinger *et al.* 2002). Why this core yielded suitable sediments to form a chronology, but Genovesa did not, may indicate a lack of volcanic activity at Bainbridge, contrasting with regular outgassing at Genovesa in the last 6000 years. Bainbridge is another hypersaline lake, fed from beneath by seawater. Its sediments are banded and inferred to reflect changes in lake chemistry driven by excess freshwater input during El Niño events. In addition to suggesting that extreme rainfall events resulted in the in-wash of clays to form siliciclastic laminae, Riedinger *et al.* (2002) suggested that weaker events may have resulted in carbonate deposition. They hypothesized that stratification of the lake by rainwater or wave-driven seawater forming a fresher floating lens of water could have led to meromixis and developed strong reducing conditions in the hypolimnion. Under such conditions carbonate would precipitate out. Thus, the frequent carbonate bands probably represent moderate El Niño events, while the siliciclastic bands represent extreme events. By looking at the composition and frequency of the bands, Riedinger *et al.* (2002) inferred the relative activity of El Niño for the last 6000 years.

A recently published lake sediment record from El Junco adds to the emerging picture of how ENSO changed through the Holocene (Conroy *et al.* 2008). Changes in grain size in this sediment core reflect changes in lake level and precipitation events, with larger-diameter particles (sand, relative to clay and silt), deposited from high intensity precipitation events. Today, intense rainfall in Galapagos is exclusively associated with El Niño events. Thus Conroy *et al.* (2008) inferred that past periods of increased grain size in the El Junco core reflect El Niño event frequency or intensity. The record of percent sand from El Junco indicates a shift toward more frequent El Niño events 4200 years ago (Conroy *et al.* 2008). A period of unusually frequent, perhaps also intense, El Niño events also occurred between 2000 and 1000 years ago.

Research in the Ecuadorian Andes at Lake Pallcacocha (4120 m altitude) (Rodbell *et al.* 1999, Moy *et al.* 2002) corroborated much of the observed pattern detected in Bainbridge and El Junco, though differing in some of the detail. Times of very active ENSO appeared to have more events (positive or negative) than in the past century, while events in other periods seemed relatively sporadic. Very active phases were documented in both records

between *c.* 2200 BP and 1000 BP, with a marked burst of activity 800–700 BP. The mid-Holocene, from 9000 to 4000 BP, was a time of low lake levels and weakened ENSO. Strong El Niño events still occurred, but were relatively rare. However, neither the Bainbridge record nor the Andean record is a perfect measure of past El Niño activity. Bainbridge is only separated from the Pacific by a 3 m high, 10 m wide berm that bears obvious signs of regular overwash. If laminations are partly caused by overwash influencing chemistry, storms unrelated to El Niño events could contribute to the observed banding. In contrast, the Andean record lies so far from the ocean and the center of upwelling that other factors could influence its history of precipitation and laminations.

Interest in ENSO activity quickly changed into a broader concern with overall climate change and the role of anthropogenic forcing. Dunbar *et al.* (1996) investigated the isotopic signature of uplifted corals in Urvina Bay, which provided a 400-year history, suggesting that the 1600s and early 1800s were cool, and that the 1700s were warm. An unusual observation was that the period 1880–1940 appeared to experience lower sea-surface temperatures. These data were not replicated in an analysis of corals from Palmyra Island, which showed a warming trend beginning around 1880, accelerating markedly after 1950 (Cobb *et al.* 2003). This trend has been found in a recent calibrated proxy record from El Junco (Conroy *et al.* 2009, 2010), and agrees with a general pattern in Pacific reef systems (Cole 2003). Such apparent disparities suggest that the Pacific Ocean is less homogeneous than we might assume. Local changes in upwelling, gyres, and surface currents can all induce local changes, without necessarily being representative of the regional picture.

Some of the latest research on El Junco draws on new proxies for past precipitation, such as hydrogen isotope ratios in fossils of the alga *Botryococcus braunii* (Zhang *et al.* 2007, Zhang & Sachs 2007). These new tools suggest relatively wet conditions during the Little Ice Age (*c.* 1400–1800), terminating with a dry event that peaked around 1870, before a trend toward wetter conditions through the 20th century (Sachs *et al.* 2009). Traditional methods are also being used, such as fossil pollen and diatoms, but these are being analyzed at much higher temporal resolution than before (*e.g.* Conroy *et al.* 2008, Restrepo *et al.* 2008, Conroy *et al.* 2009). Rather than sampling at intervals representing centuries to millennia, we are now taking samples at 3–7 year intervals. The pollen data indicate increasing transport of lowland pollen types, such as *Bursera*, up to El Junco in the last 40 years. This is interpreted as being due to increasing convection lifting pollen grains to cloud height prior to upslope deposition by rain. We hypothesize that this trend is connected to a strengthening of El Niño. Unfortunately, the local signal of vegetative response in the fossil pollen record from El Junco after 1930 is one of human-induced alteration rather than of climatic influence. Grazing animals profoundly altered the vegetation of the cone and crater, eliminating

the two most abundant elements of the pollen flora of the last 2000 years, *Acalypha* and *Alternanthera* (Restrepo-Correa 2007). The diatom record, which to date is the only Galapagos proxy that correlates with instrumental climate variables, suggests a warming trend in Galapagos SST beginning in the 19th century, with modern SST exceeding those of the last 1200 years. Gridded datasets of SST, air temperature and sea level pressure also point toward warming of the eastern equatorial Pacific and weakened Walker Circulation during the 20th century (Deser *et al.* 2010).

An uncertainty inherent in subdecadally-resolved lake sediment records is assessing season-specific variability. Wolff (2010) concludes from 44 years of Santa Cruz SST data that Galapagos SST warming is confined to the warm season. Thus, the diatom-inferred SST record might be recording a warming trend during the warm season only. Precipitation, which controls the El Junco lake level, is also most strongly correlated with SST during the warm season, while during the cool season many months have zero precipitation, leading to a non-normal distribution and weaker correlation with SST (Wolff 2010). Regardless, lakes are data reservoirs, integrating precipitation on longer than monthly time-scales, so it is more meaningful to evaluate the relationship between SST and precipitation on longer timescales when considering the relationship between SST and lake level. Our observation that lake levels have been relatively high in the last half century, and that convection has been strengthened, is consistent with Wolff's (2010) observation of increased seasonality.

The last 50 years have included some exceptionally strong El Niño events (Rein 2007), but the cumulative effects of strong ENSO variability have yet to be fully understood in the context of evaporation:precipitation balance in the El Junco system. More research is needed to reconcile the data from diatoms, pollen and the lipid deuterium:hydrogen ratio biomarker, as they were all derived from the same core.

A proverbial elephant in the room is cloud cover. All of our proxies for past climate are derived from photosynthetic organisms and all will be influenced by growing conditions, which is why they are a climate proxy. In this system where soils, temperatures at the scale of tolerance of organisms, and daylength are constant, the strongest variables are the inter-related cloud, temperature (at the scale of shaded versus brightly lit), precipitation and light.

The presence of the *garúa*, misty rain caused by stratiform cloud that hangs at *c.* 400 m on the islands, influences all climatic factors down to sea-level. *Garúa* is strongest in the cool season and during La Niña events. The highlands are frequently so cloud-shrouded that visibility is just a few meters. Under these conditions, photosynthetic organisms will be starved of light, soils will be saturated and evaporation from the lake will stall. Conversely, the warm season brings evaporation, bright

light, and soil moisture deficit. We have yet to unravel the impact that changing cloud cover has on paleoecological proxies, but note that lake hydrological modeling can be useful (Conroy *et al.* 2008).

This observation begs the question of evidence of past changes in *garúa*. We do not know for sure, but *garúa* intensity and cover have probably varied through time. That El Junco dried out during the last glacial maximum, and to some extent during the mid-Holocene dry event, could be explained by the traditional suggestion that precipitation was reduced, or that the *garúa* lifted.

Colinvaux (1972) and Newell (1973) discussed the ITCZ moving north or south to induce aridity in the islands, but the range of that movement would have to be considerable, certainly more than the *c.* 5° suggested by Sachs *et al.* (2009) for the Little Ice Age. The northward limb of the Pacific ITCZ reaches the coast of Panama at 10°N, and so a very substantial southward shift would be required to have it stay to the south of the islands. Furthermore, Glacial SSTs in the Galapagos region were probably 1–2°C cooler than modern (Lea *et al.* 2006, Otto-Bliesner *et al.* 2009), but no conclusive evidence exists regarding the possible influence of altered ENSO on the eastern tropical Pacific during the last glacial period. If the delivery mechanism of rain was still present, another possibility is that *garúa* formed less often, lasted for fewer months or for fewer hours each day. Under such conditions, rainfall coming from the ITCZ may have been largely unchanged, but the reduction in *garúa* at other times of the year may have increased evaporative loss from lakes, vegetation and soils.

A past weakening of the *garúa* is conjectural, but is a potentially testable hypothesis, and it would help to accommodate the existing data. Developing an independent measure for past *garúa* activity is one of the most important tasks ahead of us. Projections of “permanent El Niño conditions” forming in the Pacific by mid-century as a result of climate change (Cox *et al.* 2004) may be overstated (Cochrane & Barber 2009), partly because ENSO is more complex than originally thought. Indeed there is a movement towards referring to “enhanced equatorial warming”, rather than a “permanent El Niño”, because these two phenomena are not uniquely coupled (DiNezio *et al.* 2009). As we learn more of the complexity of ENSO, especially the possible shifts as Pacific temperatures warm between typical El Niño events and Modoki El Niños, where there is strong warming in the central Pacific but the warm pool of water does not extend to the Ecuadorian coast (Ashok *et al.* 2007), predicting what will or will not happen on the Galapagos Islands becomes increasingly difficult, since warming of the central Pacific is not automatically linked to decreased upwelling at the Galapagos. If the warming of the central Pacific is not accompanied by a switch toward classic El Niño conditions, the Galapagos will enter a climatic state without geologically recent analog. In terms of the long-term conservation of the island ecosystems, understanding

what happens when the *garúa* lifts may be crucial for management.

Upland areas of the inhabited Galapagos islands have become flooded by introduced invasives such as Hill Blackberry *Rubus niveus*, Quinine *Cinchona pubescens*, and Guava *Psidium guajava*. Van Leeuwen *et al.* (2008) provided a novel use for paleoecological results on the islands in their assessment of the native or exotic status of several plant species. Using pollen and macrofossils they were able to show that some presumed invasive weeds, *e.g.* *Hibiscus tiliaceus*, occurred in sediments pre-dating human.

Another unknown is the impact of the native large herbivore, the Galapagos giant tortoise *Geochelone* spp. Tortoise populations collapsed in the mid 1800s. Ships' logs show a doubling of effort needed to secure tortoises in the 1860s compared with the 1830s (Townsend 1925). Although the natural population of tortoises is unknown, their habit of visiting highland swamps is well documented. Tortoises have been shown to have an impact on island floras through both grazing and seed dispersal (Gibbs *et al.* 2008), though more research is needed to evaluate their full role in the natural ecology of the islands. These animals thermoregulate by moving in and out of water, and all shallow pools must be regarded as potential tortoise wallows. Wallowing tortoises cause tremendous bioturbation (pers. obs. on Santa Cruz). Whether tortoises ever used the high elevation bogs, which are important core sources, as wallows remains uncertain. Under modern conditions, the tortoises do not travel so high. However, if during periods of reduced precipitation, heightened evaporation or reduced cloud cover, the tortoises used these bogs, their value as paleoecological archives would be compromised. A hopeful sign is that the bogs yield sequences of ^{14}C dates that do not exhibit reversals (van Leeuwen *et al.* 2008).

Forty years of research on the Galapagos have taught us many things about the islands, and contributed to a larger debate over the importance of the Pacific to global climates. A further insight is that a bioclimatic system as simple as a low-diversity, equatorial, desert island, surrounded by a warm sea, produces paleoecological records that are easy to interpret — unless you are trying to get the answer right.

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UNNATURAL SELECTION IN GALAPAGOS: THE ROLE OF DISEASE IN DARWIN'S FINCHES (GEOSPIZINAE)

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SUMMARY

Micro-evolutionary studies, such as those of Darwin's finches (Geospizinae), have been used as indicators of rates of evolution under natural selection. Today however, such studies may be compromised by unnatural selection. Recently introduced infectious and parasitic agents in Galapagos may hamper our ability to monitor natural evolutionary change in endemic birds, by modifying such change. The opportunity to study natural selection in its iconic site may thus be lost, due to these and other forms of human environmental alteration, which may be replacing non-anthropogenic factors as the principal driver of evolution. To ensure that natural selection continues to shape the biota of Galapagos, anthropogenic impacts including introduced diseases must be managed effectively.

RESUMEN

Selección innatural en Galápagos: la influencia de las enfermedades en los pinzones de Darwin (Geospizinae). Los estudios sobre micro-evolución, tales como los de los pinzones de Darwin (Geospizinae), han sido usados como índice de evolución bajo selección natural. Sin embargo, ahora dichos estudios podrían estar comprometidos por la selección innatural. Agentes infecciosos y parasíticos introducidos recientemente en Galápagos pueden estar afectando nuestra habilidad para monitorear el cambio natural evolutivo en aves endémicas al modificar este proceso. La oportunidad para estudiar la selección natural en este sitio icónico podría perderse debido a esta y otras formas de impacto medioambiental humano, las cuales pueden estar reemplazando los factores no-anthropogénicos como motor principal de la evolución. Para asegurar que la selección natural continúe moldeando la biota de Galápagos, los impactos antropogénicos incluyendo las enfermedades introducidas deben ser manejados eficazmente.

The Galapagos Islands were instrumental to Charles Darwin's formulation of the theory of evolution by natural selection. Darwin's 1835 visit and his subsequent publication (Darwin 1859) mark the beginning of scientific fascination with the archipelago, which remains the world's laboratory of natural selection. In light of the many recent anthropogenic impacts on the Galapagos, we ask whether "natural" selection continues to shape evolutionary change on this archipelago laboratory or whether, with the escalating anthropogenic changes that include the arrival of invasive parasites and pathogens (Causton *et al.* 2006, Parker *et al.* 2006, Deem *et al.* 2008, Bataille *et al.* 2009), "unnatural" selection is now the major evolutionary force there. Here we define unnatural selection as the process whereby anthropogenic (human-induced) environmental changes dictate which organisms are best adapted to survive and transmit their genetic characteristics to succeeding generations (Palumbi 2001, Darimont *et al.* 2009, Stenseth & Dunlop 2009). Unnatural selection contrasts with natural selection only in that the selective pressures are anthropogenic, while the mechanisms of selection remain similar.

Located in the Pacific Ocean 1000 km from South America, Galapagos has yet to suffer mass anthropogenic extinctions, with an estimated 95 % of its biota extant (Gibbs *et al.* 1999). In Galapagos, scientists record evolutionary changes on macro and micro scales, the latter exemplified by the studies of Darwin's finches (Geospizinae: summarized in Grant 1999, Grant & Grant 2008) that have been used as indicators of rates of change under natural selection (*e.g.* Stenseth & Dunlop 2009). Today however, rather than providing evidence for evolution by natural selection, many of these studies may be compromised by unnatural selection. For example, unnatural selection can be seen in the beak diversification of the Medium Ground Finch *Geospiza fortis*, caused by novel food sources in a human-dominated area (Hendry *et al.* 2006), where a population of historically bimodal beak size was modified to one with unimodal beak size, while bimodality was maintained in an area relatively free of human influence. The unusually strong selection pressure from anthropogenic change may render adaptation easier to study than when evolution is driven by non-anthropogenic, usually more gradual and often stabilising, selection. If natural selection

is being overshadowed by unnatural selection even on Galapagos, the chances that evolution in the absence of anthropogenic selection is still occurring elsewhere in terrestrial ecosystems must be slight.

Species are prone to behaving in ways that are not adaptive when an environment changes suddenly, such as with the arrival of an introduced pathogen, because their behaviour is adapted to the previous evolutionary environment (Schlaepfer *et al.* 2002) and does not cover all anthropogenic contingencies. For example, in the absence of a particular parasite, birds may nest in ways that make them vulnerable to that parasite, should it be introduced, although their nesting behaviour may have been shaped by other parasites with which they have shared a long history (Loye & Carroll 1998). Unnatural selection has been recorded around the globe, associated with a variety of human activities including over-harvesting (Sasaki *et al.* 2008, Stenseth & Rouyer 2008, Darimont *et al.* 2009), introduced predators (Blackburn *et al.* 2004), and use of pesticides and drugs stimulating resistance in insects and pathogens (Palumbi 2001). Indeed, the ultimate current anthropogenic driver of evolution may be climate change (Bradshaw & Holzapfel 2006). Humans are changing the world at an unprecedented rate, modifying phenotypic traits in surviving organisms.

Even in Galapagos, introduced parasites and pathogens (Wikelski *et al.* 2004, Parker *et al.* 2006, Deem *et al.* 2008) are influencing evolution and shaping populations, as elsewhere (Strayer *et al.* 2006). As one example, the environmental changes (*e.g.* feeding stations, fresh water) that cause Medium Ground Finches to aggregate in the town of Puerto Ayora, and which resulted in beak modifications on a population scale (Hendry *et al.* 2006), will most likely also increase transmission of density-dependent pathogens. Darwin's finches may select human-populated areas since they provide benefits over more natural habitats (*e.g.* easily available food and water). However, the finches may be unable to avoid the introduced disease vectors (*e.g.* *Culex quinquefasciatus*) and pathogens that are more common in areas with fresh water (Whiteman

et al. 2005), or that are more likely to spread through a more aggregated population (*e.g.* avian poxvirus: Riper *et al.* 2002), and which thus influence their evolution.

Two recently introduced species in Galapagos, the parasitic fly *Philornis downsi* (Fessl & Tebbich 2002) and avian poxvirus (Thiel *et al.* 2005), cause mortality in endemic birds (Vargas 1987, Huber 2008). They also cause deformities of the nares and beak (Fessl *et al.* 2006, Riper & Forrester 2007) (Figs 1 & 2), hampering our ability to monitor evolutionary change in these morphological features. Further, a study on the fitness cost of avian pox for Darwin's finches on four islands found that males with pox-like lesions were significantly less likely to be pair-bonded than those without lesions (Kleindorfer & Dudaniec 2006) and thus less likely to pass their genes to succeeding generations (though other possible causes of lesions exist, such as trauma, bacterial or fungal infections: Riper & Forrester 2007). Another study of the Medium Ground Finch found that nestlings parasitized by *P. downsi* had smaller beak depths compared to unparasitized nestlings (Huber 2008). Surviving parasitized nestlings probably also have reduced fitness, based on their lower haemoglobin content and beak deformities (Dudaniec *et al.* 2006, Fessl *et al.* 2006). Therefore, Medium Ground Finches with larger beak depth may have an adaptive advantage when under pressure from these parasites. Alternatively, it is possible that nestlings surviving *P. downsi* infestations grow less (including their beaks) than they would have without parasites due to the reallocation of resources to fighting the infection: this would result in a phenotypic change without genotypic selection for beak size. These examples suggest a need for long-term studies of the impacts of invasive pathogens on the evolution of Darwin's finches and other taxa.

In 2009, a year of Darwin anniversaries, it appears that the opportunity to study natural selection in its iconic site (Boag & Grant 1981, Grant & Grant 1989) may soon be lost, due to unnatural selection by invasive pathogens and parasites, and other forms of human environmental alteration. Such anthropogenic selection



Figure 1. An adult male Common Cactus Finch *Geospiza scandens* with deformity to the beak and nares caused by *Philornis downsi*.



Figure 2. An adult Woodpecker Finch *Cactospiza pallida* with avian pox lesions on dorsal mandible and lower eyelid.

may overshadow, confound and ultimately replace non-anthropogenic factors as the principal driver of evolution. To prevent further degradation of natural selection, global concern for the conservation of Galapagos ecosystems must be translated into effective management of anthropogenic impacts, including introduced diseases. Preventing the arrival of more parasites and pathogens to the islands, and mitigating the impacts of those already introduced, are imperative to ensure that natural selection continue to shape the biota of Galapagos.

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Galapagos Research

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