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RESEARCH ARTICLES

ALKALOIDAL PROTECTION OF *UTETHEISA GALAPAGENSIS* (LEPIDOPTERA: ARCTIIDAE) AGAINST AN INVERTEBRATE AND A VERTEBRATE PREDATOR IN THE GALAPAGOS ISLANDS

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SUMMARY

The Galapagos endemic moth *Utetheisa galapagensis* has been shown to sequester pyrrolizidine alkaloids from its host plants in the genus *Tournefortia* (Boraginaceae). We here assess the palatability of *U. galapagensis* adults to sympatric invertebrate and vertebrate predators. Adult *U. galapagensis* and *Pilocrocis ramentalis* (Pyralidae) controls, were offered to orb-weaving spiders *Eustala vegeta* and female lava lizards, *Microlophus pacificus*. The spiders' reactions to the two types of prey were highly stereotyped; invariably the controls were eaten and the *U. galapagensis* were cut from the web and released. In comparison, when offered to female lava lizards both *U. galapagensis* and the pyralid controls were usually consumed. However, the lava lizards sometimes displayed rejection behavior with *U. galapagensis* and the time spent handling this species was significantly greater than for controls. Our results indicate that *U. galapagensis* relies on alkaloidal defense to protect it from nocturnal arachnid predators. Against diurnal lizards crypsis is likely their major defense since alkaloidal sequestration is only marginally effective in protecting them from these predators.

RESUMEN

Protección por alcaloides contra predadores vertebrados e invertebrados de *Utetheisa galapagensis* (Lepidoptera: Arctiidae) en las islas Galápagos. La mariposa endémica de Galápagos *Utetheisa galapagensis* secuestra alcaloides de su planta huésped del género *Tournefortia* (Boraginaceae). Hemos probado el sabor de adultos de *U. galapagensis* con predadores simpátricos de vertebrados e invertebrados. Adultos de *U. galapagensis*, y como control, de *Pilocrocis ramentalis* (Pyralidae), fueron ofrecidos a arañas tejedoras *Eustala vegeta* y a hembras de lagartijas de lava *Microlophus pacificus*. La reacción de las arañas a los dos tipos de presa fueron altamente estereotipadas; invariablemente el control fue comido y las *U. galapagensis* fueron liberadas luego de ser cortada la red. En comparación, cuando fueron ofrecidas a las hembras de lagartijas de lava, *U. galapagensis* y el control Pyralidae fueron usualmente consumidos. Sin embargo, la lagartija de lava algunas veces tuvo un comportamiento de regurgitación con *U. galapagensis* y el tiempo pasado manipulando esta especie fue significativamente mayor que para el control. Nuestros resultados indican que *U. galapagensis* tiene defensas por alcaloides para protegerse de predadores como arañas nocturnas. Contra las lagartijas diurnas la coloración críptica parece ser su mayor defensa desde que el secuestro de alcaloides es solo parcialmente efectivo para protegerlas contra esos predadores.

INTRODUCTION

Members of the cosmopolitan tiger moth genus *Utetheisa* are frequently brightly colored (Fig. 1) and are considered diurnal and aposematic (Holloway 1988). The latter contentions have been tested with larval and adult *U. ornatrix* L., a species known to sequester defensive pyrrolizidine alkaloids (PAs) from its larval host plants, legumes of the genus *Crotalaria* (Conner *et al.* 1981). By virtue of their bad taste, sequestered PAs protect larvae,

pupae, and adults from invertebrate and vertebrate predators (Eisner & Eisner 1991, Eisner *et al.* 2000, Eisner 2003, Eisner & Meinwald 2003, Rossini *et al.* 2004) and since the alkaloids can be passed transovarially, they protect the egg stage as well (Bezzerides *et al.* 2004, Hare & Eisner 1993). Diurnal predators are also apparently capable of learning to discriminate against the gold, black and white pattern of the larvae and the pink, black and white pattern of the adults as aposematic warnings of their underlying PA defense (Eisner 2003).

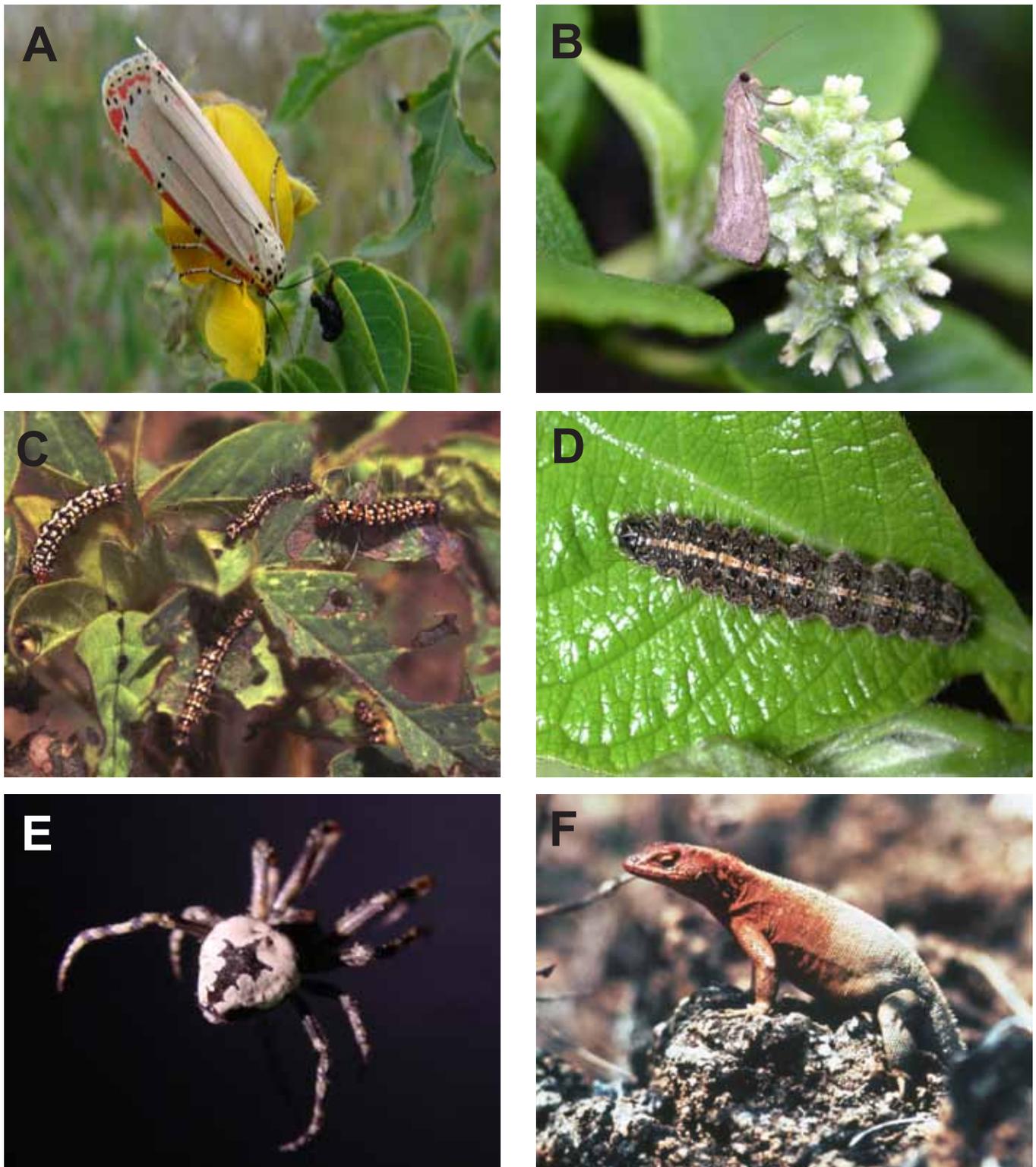


Figure 1. Comparison of the aposematic adult and larval stages of *Utetheisa ornatrix* (A and C) with the cryptic adult and larval stages of *Utetheisa galapagensis* (B and D). Predators used to assess moth palatability: (E) the nocturnal arachnid *Eustala vegeta* (alcohol preserved specimen) and (F) the diurnal lava lizard *Microlophus pacificus*.

In the Galapagos Archipelago there are three endemic species of *Utetheisa* that do not fit the general *ornatrix* pattern. *U. galapagensis* (Wallengren), *U. perryi* Hayes and *U. devriesi*

Hayes can all be considered cryptic (Fig. 1). Larvae of all three species are drab in color and secretive in habit. Adults are brownish grey and blend in with their environs.

Roque-Albelo *et al.* (2002) posed four possible explanations for this deviation from the aposematic norm: (1) the endemic species may be chemically protected (unpalatable) yet primarily nocturnal, rendering warning coloration unnecessary; (2) they may be chemically protected and diurnal and use crypsis as a second line of defense; (3) they may be palatable (not chemically protected), diurnal and employ crypsis; (4) they may be palatable, nocturnal and non-aposematic. Roque-Albelo *et al.* (2002) found that one of the endemics, *U. galapagensis*, sequesters PAs not from *Crotalaria* but instead from *Tournefortia* species (Boraginaceae), including *T. rufo-sericea* Hook. f. Both plant and insect contain the PA indicine and related alkaloids that are potentially protective. However, *Tournefortia* alkaloid-laden *U. galapagensis* have never been tested to determine their degree of protection against natural predators. We here describe simple spider and lizard bioassays with predators and prey in their natural habitat.

METHODS

Adult *U. galapagensis* were offered as prey items to an endemic orb-weaving spider, *Eustala vegeta* (L. Koch) Simon (Araneidae), on Isabela island, as well as to an endemic lava lizard, *Microlophus pacificus* Steindachner (Kizirian *et al.* 2004), on Pinta island (Fig. 1). Lava lizards were chosen because they are a diurnal predator known to include adult moths in their diet (Stebbins *et al.* 1966). All bioassays were conducted in the species' natural habitats. Spiders were identified by Dr. Léon Baert, Departement Entomologie, Koninklijk Belgisch Instituut voor Natuurwetenschappen.

Spider Bioassays

For the first set of experiments, adult *U. galapagensis* and controls (*Pilocrosis ramentalis*, Lederer: Pyralidae) were collected on 12 and 13 March 2005, at an ultraviolet light at 850 m elevation on the eastern slope of Alcedo volcano, Isabela island. The habitat was the humid zone of the volcano dominated by *Psidium galapageium* Hook. f. (Myrtaceae), *Tournefortia pubescens* Hook. f. and *Scalesia microcephala* B.L. Rob. (Asteraceae). Moths were collected directly before their use in spider bioassays. *Eustala* were located in the immediate surroundings of the moth collecting site. Only spiders with fresh webs were used in the bioassays.

Bioassays were carried out after dusk. Each began by placing a randomly chosen *U. galapagensis* or pyralid within the lower half of a spider's web. Once the spider had either cut the moth from its web or consumed the moth, in part or in whole, and had returned to the hub of its web, the alternate prey species was placed in the web. The reaction of each spider to both prey items was recorded in infrared digital video for later analysis (Sony Digital Handycam DCR-TRV36). No spider was used for more than one presentation of *U. galapagensis* and one presentation of a control pyralid.

Lizard Bioassays

Adult *U. galapagensis* and pyralid controls were collected on 17 and 18 March 2006, at an ultraviolet light at 421 m elevation on the southern slope of Pinta island. The habitat was transition forest dominated by *Pisonia floribunda* Hook. f. (Nyctaginaceae), *Zanthoxylum fagara* (L.) Sarg. (Rutaceae), and *Tournefortia rufo-sericea* Hook. f. (Boraginaceae). Moths were collected and housed in plastic vials until bioassays could be performed the following day.

Female lava lizards *Microlophus pacificus* were located in our camp and along adjacent trails. Although *U. galapagensis* are primarily nocturnal they frequently take flight when disturbed during the day. This renders them susceptible to attack by diurnal predators like lava lizards.

Bioassays were carried out at midday. Each began by offering a lizard one control pyralid moth and one *U. galapagensis* in random order. One wing was clipped from each moth to prevent escape. The alternate moth was then presented to the lizard approximately 1 min. after the first interaction had terminated. The reaction of each lizard to both prey items was videotaped using the video camera described above, but with natural illumination. Handling time was determined by field-by-field analysis of the videotape and was defined as the time between a lizard's first contact with the prey and when the prey was completely consumed by the lizard (defined as the disappearance of any body parts protruding from the lizard's moth).

Statistics

A Fisher Exact Test (Sokal & Rohlf 1981) was used to compare the reaction of both lizards and spiders to *U. galapagensis* and pyralid controls. To compare mean handling times we used a paired *t*-test assuming unequal variance (SPSS® 14.0).

RESULTS

Spiders

The spiders' reactions to the two types of prey item were stereotyped. When a pyralid was placed in the web, the spider tensed the web and located the prey item. It then rushed to the moth, palpated it, attacked and immediately began to consume the moth. After a feeding bout, lasting a variable amount of time, the spider wrapped the moth in silk and then either continued to feed or carried the prey to the hub of the web where it hung the moth for later feeding. The reaction to *U. galapagensis* was strikingly different. The spider again rushed to the moth, contacted the moth with its mouthparts, apparently tasting it, and instantly withdrew a variable distance. After a moment the spider began to manipulate the moth with its legs and mouthparts to detach the moth from the web. *U. galapagensis* specimens were invariably released (Table 1). The probability of this distribution of results is highly significant (Fisher Exact Test $P < 0.01$).

Table 1. Palatability of *Utetheisa galapagensis* and pyralid controls to *Eustala vegea* spiders. Left column gives the number of the individual spider tested. + indicates the spider fed on and wrapped the moth; – indicates it rejected the moth.

Spider	Pyralid control	<i>Utetheisa galapagensis</i>
1	+	no data
2	no data	-
3	+	-
4	+	-
5	no data	-
6	+	-
7	+	-
8	+	-
9	+	-
10	+	-
11	+	-

The behavior of each moth species may also have contributed to the interaction. The pyralids clearly struggled with the spider, and the spider responded by wrapping the moths in silk. The *U. galapagensis* froze, rarely struggled and were consequently not wrapped in silk.

Lava Lizards

When a moth specimen was offered the lizard either responded immediately or at the first sign of fluttering of the moth. The attack was swift and visually directed. The lizard proceeded to mouth the specimen while reorienting it for swallowing. All control pyralids were eaten and all but two of the *U. galapagensis* were also consumed (Fisher Exact Test $P > 0.05$). However, the lizards showed greater reluctance to swallow the *U. galapagensis*, as manifest in a significantly longer handling time (4.97 ± 1.64 s for pyralid controls and 12.79 ± 5.51 s for *U. galapagensis*; t -test, $P < 0.01$; Table 2). The two lizards that did not eat the *U. galapagensis* showed classic rejection behavior. They attempted to scrape the specimen from their mouths with their forelegs

Table 2. Palatability of *Utetheisa galapagensis* and pyralid controls to lava lizards *Microlophus pacificus*. Left column gives the number of the individual lizard tested. The other columns indicate the time (seconds) between the lizard's first contact with the moth and the disappearance of the prey item.

Lava lizard	Pyralid control	<i>Utetheisa galapagensis</i>
1	4.58	7.94
2	4.80	13.17
3	2.67	12.40
4	5.60	not eaten
5	4.93	24.57
6	2.07	12.13
7	5.49	11.00
8	6.14	14.80
9	7.77	not eaten
10	5.64	6.27

and frequently wiped their mouths on the substrate after rejecting the specimen. However, if the released moth fluttered again, the lizard reinitiated the attack sequence. One *U. galapagensis* was attacked and released three times in rapid succession. No learning was evident.

DISCUSSION

It is clear from even this small number of presentations that *U. galapagensis* is highly unpalatable to *Eustala vegea*. It seems probable that the unpalatability is due to sequestered PAs, which have previously been shown to be present in both the food plant and bodies of male and female *U. galapagensis* (Roque-Albelo *et al.* 2002). PAs are extremely effective repellents for arachnids (Brown 1984, Eisner 2003) and the behavioral responses of *Eustala vegea* are identical to those seen with *U. ornatix* and the orbweaving spider *Nephila clavipes* L. (Eisner 2003). The PAs of *U. galapagensis* were apparently less effective against the lava lizards. It is unlikely that the moth would survive the intense attack of a lava lizard even if rejected. The rapid, motion-triggered attack of the lava lizard places a premium for the moth on resting motionless during the day. Handling of *U. galapagensis* also frequently elicits "freezing" behavior, which may be adaptive in this context.

Thus, *U. galapagensis* appears to incorporate components of hypotheses 1 and 2 (in our Introduction) proposed to explain loss of aposematism in Galapagos *Utetheisa* (Roque-Albelo *et al.* 2002). The moths are primarily nocturnal and chemically defended: strongly against a nocturnal orb weaving spider and mildly against a diurnal lizard. They appear to employ crypsis against diurnal vertebrate predators since the alkaloidal defense is less effective against them. Future experiments with insectivorous birds, such as Galapagos mockingbirds, may clarify the degree of unpalatability of this moth to diurnal predators.

It remains to be seen whether the aposematically colored *U. ornatix* is the closest relative of the three endemic, cryptic species. If this is the case, the switch to PA-containing *Tournefortia* would be a simple transition from one PA hostplant species (*Crotalaria*) to another (*Tournefortia*), with the loss of aposematism and the species becoming nocturnal on the islands. Alternatively, *U. galapagensis* may have arisen from a cryptically colored nocturnal ancestor with characteristics similar to those of all three endemic species. Phylogenetic and biogeographic analyses may ultimately answer these questions.

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THE 1997–8 EL NIÑO AND THE GALAPAGOS TORTOISES *GEOCHELONE VANDENBURGHI* ON ALCEDO VOLCANO, GALAPAGOS

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SUMMARY

Body mass changes, mortality and nest and egg loss of the Galapagos tortoise *Geochelone vandenburghi* were studied on Alcedo Volcano, Isabela Island, before, during and after the El Niño event of 1997–8. The results suggest that fewer tortoises in the pre- and post-Niño periods gained body mass than lost, while during the El Niño event itself the tortoises gained mass. Before and after the El Niño, there was no mortality attributable to flooding in the ravines on the slopes of the volcano, but during the El Niño event 36 tortoises were found dead in the ravines. This is < 1 % of the total population. Nest and egg loss due to fungus damage was low (<10 %) in the pre- and post-Niño periods, but during the event a significantly higher proportion (80 % of 76 eggs) were destroyed by fungal infection.

RESUMEN

Cambios en la masa del cuerpo, mortalidad y la pérdida de huevos de la tortuga de Galápagos *Geochelone vandenburghi* fueron estudiados en el Volcán Alcedo, Isla Isabela, antes, durante y después del acontecimiento El Niño de 1997–8. Los resultados sugieren que las tortugas en el pre- y post-Niño incrementaron el peso y más individuos disminuyeron el peso. Durante El Niño, más tortugas incrementaron el peso y menos animales disminuyen el peso. Antes y después de El Niño no hubo mortalidad por causa de inundación en las encañadas en las faldas del volcán, pero durante el acontecimiento El Niño se encontró 36 tortugas muertas en las encañadas. Esta fue estimada en < 1 % de la población total. Daño a los nidos y huevos por hongos fue baja (<10 %) en los periodos pre- y post-Niño, pero durante el evento una cantidad significativamente mayor (80 % de 76 huevos) fue destruido por infección de hongos.

INTRODUCTION

Galapagos tortoises *Geochelone* spp. are the dominant native herbivores in the Galapagos archipelago. On Alcedo Volcano, Isabela Island, occurs the largest remaining population, *G. vandenburghi* (Fowler 1983, de Vries 1984, Enriquez 1984, Cayot 1987), estimated at between 10,000 and 12,000 individuals (Márquez *et al.* 2004). Between 1990 and 2006 the tortoises of Alcedo suffered competition for food from an abundant population of feral goats *Capra hircus* (Márquez *et al.* 2004), although an eradication program begun in 2004 had almost completely eliminated goats from Alcedo by early 2006. The effects of this competition might be exacerbated by natural phenomena such as extreme drought or extremely rainy years, such as those caused by an El Niño Southern Oscillation event. El Niño is an atmospheric-ocean phenomenon associated with heavy rains in the eastern Pacific, where it is often followed by a dry year (La Niña), both of which can affect the fauna and flora of Galapagos (Snell & Rea 1999, Cayot 1985). However, the effect of El Niño on the Galapagos tortoises has not been documented.

The present report evaluates a possible effect on the tortoises of Alcedo Volcano by the strong El Niño event of 1997–8, via effects on body mass, mortality from drowning and injury from falling into rushing waters in ravines, and loss of eggs as a result of contamination by fungus in the nests. We compare the body mass of the tortoises, egg losses and mortality in the population of the Alcedo tortoises for three two-year periods: prior to the El Niño event ("Pre-Niño" 1995–6), during the El Niño event (1997–8), and following it ("Post-Niño" 1999–2000).

METHODS

Study area

Alcedo Volcano is located in the centre of Isabela Island, with a maximum elevation of 1128 m and an area of 798 km² (Black 1973). It is principally covered with arid woodlands, although with areas of more dense and humid vegetation on the higher slopes, and with some grassland near the crater edge. Introduced mammals that shared habitat with the tortoises and compete with them included goats and donkeys *Equus asinus*. Black rats *Rattus*

rattus and feral cats *Felis catus* also occur in the area and are predators on newly-hatched tortoises. Alcedo is the only Galapagos volcano that has a reproductive population of tortoises on the interior, edge and flanks of the crater.

Tortoise marking and monitoring

Tortoises were individually marked with permanent branded numbers on the fourth left plate and with a passive integrated transponder (PIT) tag injected under the skin of the left hind leg. The tortoises were monitored twice per year from November 1995 to November 2000, and at each visit, tortoises that had not been identified previously were marked. Over the study period, 961 tortoises were marked and 540 of them relocated and re-measured. Monitoring transects were established and searched during each survey on the east slope, and on all of the crest and interior of the crater.

Information collected

The locations of all tortoises encountered, whether alive or dead, and all tortoise nests, were recorded using Global Positioning System receivers and mapped using a Geographic Information System. All live tortoises encountered were sexed and aged (male, female or juvenile) as far as possible (the sex of young tortoises cannot be determined; therefore, they were counted as juveniles). They were weighed using a tetrapod frame and an electronic balance of capacity 1 t.

Tortoises found dead were divided into three categories of likely mortality:

- a) Accidental death by falling, with the carapace semi-destroyed but the remains not dispersed (Fig. 1).
- b) Accidental death by floodwaters (tortoises falling into or being trapped in ravines filled with waters from heavy rains), with the carapace disarticulated and remains dispersed along the ravines.



Figure 1. Partially destroyed carapace of a tortoise, possibly killed in a fall or by being washed down a ravine by flood waters (live juvenile tortoise walking in the foreground).

c) Death with the carapace intact, with no parts broken, its keratin plates in place and upright (plastron down) at the presumed site of death, the cause of mortality being unknown but likely not from falling or flooding. This included tortoises found dead at the summit of the crater (Fig. 2).

The carapace of a tortoise was considered destroyed when remains were scattered, or it was broken at the junction of carapace and plastron or frontally or posteriorly. The remains were classified as male, female or juvenile. Although tortoise poaching occurs on Isabela Island, none of the tortoise mortality found during this study was a result of humans killing the tortoises.

Search for dead tortoises in ravines

Six ravines were selected for repeated intensive search for tortoise remains. A transect of 300 m was established in each ravine, for a total of 1.8 km total transect length. The transects were searched each time the tortoises were monitored. All tortoises found dead on the transects were evaluated as described above.

Tortoise nests and eggs

Tortoise nests were excavated, as part of the captive-rearing program carried out by the Galapagos National Park and Charles Darwin Research Station. Eggs were examined to determine if they were broken, infertile, or had been killed by fungus. Signs of fungal infection included the egg exterior being covered by fine, soft, gray hairs and its interior showing dark black spots. Eggs were determined to be infertile when their exterior appeared normal, but following incubation (as part of the captive-rearing program) the egg failed to hatch and proved to contain no embryo. Eggs that subsequently hatched in the captive-rearing program incubators were considered normal.



Figure 2. Intact carapace of a tortoise that died of natural but unknown causes.

Study periods

The Pre-Niño study period encompassed three monitoring trips, 9–20 November 1995, 23–29 May 1996 and 26 November to 3 December 1996. Rainfall during this period at the Charles Darwin Research Station weather station in Puerto Ayora, Santa Cruz Island, was 251.7 mm, and the average temperature was 23.2°C. During the El Niño event of 1997–8, monitoring trips were made on 4–9 May and 18–24 November 1997, and 18–25 May and 9–17 November 1998. During the El Niño, the rainfall was 1703.8 mm, and the temperature was 25.6°C. In the “Post-Niño” period, monitoring trips were made in 12–19 November 1999 and 4–9 November 2000. During the Post-Niño, rainfall at Puerto Ayora was 166.1 mm and the temperature was 23.4°C.

RESULTS

Changes in body mass

During the Pre-Niño period 10 of 34 (29%) tortoises recaptured showed an increase in body mass of 1–10% (Table 1), whereas the remaining 24 (70.59%) showed a decrease in body mass of 1–15%, in relation to their mass in November 1995. During the El Niño event, 39 of 50 (78%) of the tortoises increased their mass over their initial (Nov 1995) weight, and the remaining 11 (22%) decreased. In the Post-Niño 17 of 28 (61%) tortoises decreased their mass with respect their mass over their initial weighing, and 11 (39%) increased. The proportions showing change in mass in different directions were significantly different between the three periods ($\chi^2_2 = 22.3, P < 0.0001$).

Comparing the three periods, the groups of tortoises that lost and increased mass before or after the El Niño event were not different with regard to average mass lost or gained among the three events (factorial ANOVA, $F = 9.48, P > 0.05$). In the Pre-Niño and Post-Niño, the average changes in mass were similar (Table 1), while during the El Niño event the average value for change in mass was greater, although not significantly so ($t_{82} = 0.71, P > 0.50$; Table 1).

Mortality of tortoises

In the two years of the Pre-Niño period (1995–6), dead tortoises with destroyed carapaces were not recorded either in the interior or along the 300 m of transects in any of the ravines surveyed. During this period four dead

tortoises but with the carapace intact were recorded outside the six ravines. During the two years of the El Niño event (1997–8) at least 36 dead tortoises (29 adults and seven juveniles) with the carapace destroyed were recorded, all in the interior of the six ravines. No dead tortoises were recorded outside the ravines during the El Niño. During the Post-Niño (1999–2000) no recently-dead tortoises were recorded inside the ravines, but nine dead tortoises with intact carapaces were encountered outside the ravines. The number of dead tortoises by period and site were different between the Pre-Niño, El Niño, and Post-Niño ($\chi^2_5 = 26.9, P < 0.001$). The number of dead tortoises during the El Niño event is $< 1\%$ of the total population.

At El Geiser on the interior slope of the volcano crater at *c.* 970 m altitude, on two occasions tortoises were observed to fall, with the impact destroying the carapace and the tortoise dying within a few minutes. At this site, five mortalities due to falls were recorded in the Pre-Niño, nine due to falls during El Niño, and four due to falls in the Post-Niño.

Nests and eggs destroyed

During the El Niño period, 11 tortoise nests containing a total of 76 eggs were excavated, of which 61 eggs (80%) were decomposed through damage by fungus. In the Pre-Niño, five nests containing 40 eggs, and in the Post-Niño four nests with 32 eggs were excavated, but in none of those nests were the eggs decomposed or showing evidence of fungus. The numbers of damaged and viable eggs in the three events were significantly different ($\chi^2_4 = 80.7, P < 0.0001$). During the El Niño period, broken eggs were discovered dispersed over approximately 1 ha at the end of one of the ravines on the southwestern interior of the crater. These eggs were presumably destroyed when washed down from the ravine. In the Pre-Niño and Post-Niño at the same nesting site, no damaged eggs or eggshells were seen.

DISCUSSION

Changes in body mass

Before the El Niño an equal number of tortoises increased mass as decreased, while during the El Niño and Post-Niño, the number that increased body mass was greater than the number that decreased. The averages of increase and decrease are not different among the three events. This suggests that the El Niño and Post-Niño are favorable

Table 1. Changes in body mass (kg) of Galapagos tortoises *Geochelone vandenburghi* during Pre-Niño, El Niño and Post-Niño periods on Alcedo Volcano.

	Mass gain in tortoises showing increased mass			Mass loss in tortoises showing decreased mass			n Total
	mean \pm SD	Range	n	mean \pm SD	Range	n	
Pre-Niño (1995–6)	18.28 \pm 16.55	1.26–43.54	10	11.74 \pm 12.06	0.2–47.4	24	34
El Niño (1997–8)	21.49 \pm 22.63	1.0–93.99	39	14.44 \pm 14.17	1.25–54.71	11	50
Post-Niño (1999–2000)	18.06 \pm 17.02	0.1–66.84	11	11.07 \pm 7.21	0.2–27.75	17	28

for gain in body mass to the majority of tortoises, while in the Pre-Niño 71% of the individuals are benefited by mass gain and the rest maintain their mass or decrease. The maintenance of an elevated mass after the El Niño probably resulted from the exuberant vegetation that grew as a result of the El Niño event, which provides abundant food for the tortoises. The tortoises increase their body mass when there is an abundance of food and water during and for several years following the El Niño event. According to MacFarland *et al.* (1974), Fowler (1983), Beaman (1985), Cayot (1985), and T. Fritts (pers. comm.), during the 1982–3 and 1997–8 El Niño events, tortoises gain body mass and size when El Niño events occur and immediately afterward.

The physiological and behavioral factors involved in changes in body mass in the tortoises are not known, but are thought to include: 1) a capacity to self-regulate body mass, in accordance with the availability of food and environmental conditions; 2) egg-laying (females); 3) reduced activity (including foraging) when faced with reduced availability of succulent vegetation, reduction in weight of body water, and poor health. They increase mass when they are foraging constantly. Adult tortoises from the islands of Pinta and Española changed mass over four years in captivity (unpubl. data), probably not as the result of El Niño nor of lack of appropriate food, but reflecting natural physiological changes that occur in these animals.

Mortality of the tortoises

At least 36 adult male and females and juvenile tortoises were found dead in the six ravines which were regularly monitored, possibly as a result of flooding caused by heavy rains. To cool off, tortoises partially submerge themselves in pools of water, usually found in the bottoms of ravines. They may also sleep in ravines, and are not able to escape when the waters begin to rise. It is thought that some of the tortoises were killed when being washed down the ravines and smashed against rocks. Others were probably killed by falling on material loosened by the rains, down slopes and into the ravines. In other populations tortoises have been found dead as a result of bacterial septicemia and intestinal parasites (unpubl. data, Snell & Rea 2000). In captivity on Santa Cruz Island, tortoises have died from pneumonia, infections of the intestinal tract or respiratory system, accidental overturning, and injuries resulting from moving (unpubl. data). In tortoises that die of natural causes, particularly as a result of disease, the carapace is not damaged immediately, although it may disintegrate into pieces more than a year after the death of the animal.

Nest and eggs destroyed

On Alcedo Volcano, some female tortoises lay in nests within or alongside the ravines, where they can be destroyed by floodwaters. Flooding damage probably only affects tortoise populations nesting on the steeper

slopes of volcanoes on Isabela Island. There was also an increase in fungal infections in the clutches during El Niño years.

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DISTRIBUTION OF FIRE ANTS *SOLENOPSIS GEMINATA* AND *WASMANNIA AUROPUNCTATA* (HYMENOPTERA: FORMICIDAE) IN THE GALAPAGOS ISLANDS

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SUMMARY

The Little Fire Ant *Wasmannia auropunctata* (Roger) and the Tropical Fire Ant *Solenopsis geminata* (Fabricius) are considered two of the most serious threats to the terrestrial fauna of Galapagos, yet little is known about their distribution in the archipelago. Specimens at the Charles Darwin Research Station and literature were reviewed and distribution maps compiled for both species. *W. auropunctata* is currently recorded on nine islands and six islets and *S. geminata* is recorded on seven islands and six islets. New locations were registered, including the first record of *W. auropunctata* on Española and North Seymour islands, and of *S. geminata* on Fernandina Island. We recommend further survey, especially in sensitive areas, in order to plan management of these species.

RESUMEN

La Pequeña Hormiga de Fuego *Wasmannia auropunctata* (Roger) y la Hormiga Tropical de Fuego *Solenopsis geminata* (Fabricius) son especies introducidas consideradas de mayor amenaza a la fauna terrestre de Galápagos, sin embargo poco se conoce sobre su distribución en el archipiélago. A través de consultas bibliográficas y revisiones a los especímenes de la Estación Científica Charles Darwin, se determinó su actual distribución. *W. auropunctata* esta registrada en nueve islas y seis islotes y *S. geminata* se encuentra en siete islas y seis islotes. Se registraron nuevas localidades incluyendo el primer record de *W. auropunctata* en la isla Española y el islote Seymour Norte, y de *S. geminata* en la isla Fernandina. Se recomienda una mayor investigación en cuanto a su distribución en el campo, especialmente en áreas sensibles, a fin de realizar el control de estas especies.

INTRODUCTION

Ants are among the most efficient and widely distributed insect predators (Reimer 1994, Tsutsui & Suárez 2003). Highly aggressive, with a powerful sting and large unicolonial populations, fire ants displace other invertebrates and are among the most successful invasive ants.

Little is known about the ant fauna of the Galapagos Islands (Brandão & Paiva 1994). Of the 48 species reported to date, 30 were probably introduced by humans (HH unpubl.). The fire ants, *Solenopsis geminata* Fabricius and *Wasmannia auropunctata* Roger were first recorded in Galapagos at the beginning of the 20th century (Williams & Whelan 1991, 1992). Several studies have evaluated the impact of the Little Red Fire Ant *W. auropunctata* in Galapagos, although little is known about its current distribution. On Santa Cruz (Lubin 1984) and Marchena islands (Mieles 2002), invertebrate diversity is lower in areas infested by *W. auropunctata*. The Tropical Fire Ant *S. geminata* is less well documented in Galapagos especially in regard to its impact and distribution. *S. geminata* has been suggested to be a threat to the hatchlings of endemic reptiles and birds (Williams & Whelan 1991, Tapia 1997) but studies have not been carried out to confirm this.

Because of their known impacts in other parts of the world and in Galapagos (Causton *et al.* 2006) an evaluation of their status in Galapagos is required, in order to determine appropriate management actions.

The purpose of this study was to determine the distribution of *S. geminata* and *W. auropunctata* in Galapagos and identify necessary future studies.

METHODS

Material (c. 1800 collections) deposited in the Invertebrates Collection at CDRS, and literature and field reports were reviewed in June 2005. Much of the material was identified for the first time. Previous identifications were confirmed using taxonomic keys and ant databases (e.g. Ant Web <http://www.antweb.org>).

RESULTS

Solenopsis geminata was recorded on seven islands (Fernandina, Floreana, Isabela, San Cristóbal, Santa Cruz, Santa Fe, and Santiago) and six islets (Baltra, Albany, Bainbridge 1, Mao, Marielas 1 and 2) (Table 1, Fig. 1). The Fernandina record is a new island for this species, represented by specimens collected in 2005 from Punta Mangle.

Table 1. Distribution of *Solenopsis geminata* on the Galapagos Islands.

Island	Locations	First record	Reference
Albany	None specified	2004	CDRS
Bainbridge 1	None specified	2000	CDRS
Baltra	None specified	2005	CDRS
Fernandina	Punta Mangle	2005	CDRS
Floreana	Asilo de la Paz, Cerro Pajas, Las Palmas, Punta Cormorant	1919	Wheeler 1919
Isabela	Caleta Iguana, Cerro Azul, Cinco Cerros, Los Tintos, Punta García, San Pedro, Sierra Negra, Tortuga Negra, Alcedo	1981	Lubin 1984
Mao	None specified	2004	CDRS
Marietas 1, 2	None specified	1998	CDRS
San Cristóbal	EL Progreso, La Lobería, Puerto Chino, Puerta Negra	1891	Brandão & Paiva 1994
Santa Cruz	Basurero Municipal, Bellavista, El Camote, Cerro Crocker, Cerro Dragón, Media Luna, Punta Nuñez, Puerto Ayora, Tortuga Bay	1982	Meier 1994
Santa Fe	La Caleta	1986	CDRS
Santiago	None specified	2006	Causton <i>et al.</i> 2006

Wasmannia auropunctata has a wider distribution in Galapagos and is reported from nine islands and six islets (Table 2, Fig. 2). Prior to this study it was reported from Floreana, Isabela, Marchena, Pinzón, San Cristóbal, Santa Cruz, Santa Fe, Santiago and the islets Albany, Cousins, Eden, Mao and Champion. As a result of this study new records were found on Española Island and North Seymour islet. Collection records for these two islands date back to 1998.

DISCUSSION

To date, both species are found on most of the large islands in the centre of the archipelago and some of their associated islets. The extent of the distribution of *S. geminata* on Fernandina and of *W. auropunctata* on Española and North Seymour, newly registered during this study, should be determined as soon as possible in order to plan appropriate management. These islands are relatively pristine and

therefore especially vulnerable to introduced species, so the ecological consequences of the fire ants could be disastrous.

Islands with a high number of records are probably the result of greater collecting effort rather than reflecting the current abundance and distribution of the fire ants. Indeed, because ant surveys are incomplete, recent reports may not represent the date of arrival of ants at a location and they may have been resident for many years before that. For example, given that *S. geminata* was first reported from San Cristóbal in 1891 (Brandão & Paiva 1994) and that this species uses nuptial flights to establish new colonies, the lack of records from some islands suggests a need for further sampling rather than a lack of dispersal. On the other hand, some reports have been confirmed as truly recent introductions, such as the new report of *S. geminata* at Punta Mangle, Fernandina, a location that was monitored for fire ants in 1998 (L. Roque-Albelo & C. Causton unpubl.).

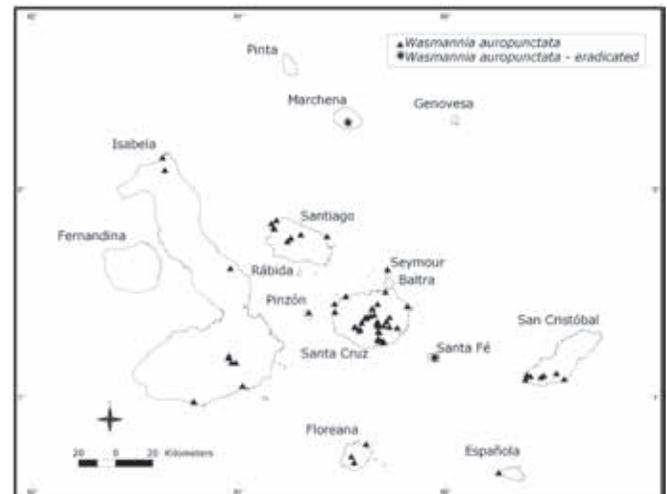
**Figure 1.** Distribution of *Solenopsis geminata* in Galapagos.**Figure 2.** Distribution of *Wasmannia auropunctata* in Galapagos.

Table 2. Distribution of *Wasmannia auropunctata* on the Galapagos Islands.

Island	Locations	First record	Reference
Albany	None specified	2000	CDRS
Cousins	None specified	2000	CDRS
Champion	None specified	2006	Causton <i>et al.</i> 2006
Edén	None specified	1999	CDRS
Española	Punta Suárez	1998	CDRS
Floreana	Asilo de la Paz, Cerro Pajas	1972	Silberglied 1972
Isabela	Caleta San Pedro, Las Merceditas, Punta Albermarle, Puerto Villamil, Playa Tortuga Negra, San Pedro, Santo Tomás, Sierra Negra, Los Tintos, Alcedo, Wolf	1976	CDRS
Mao	None specified	2000	CDRS
Marchena	Playa Negra	1988	Roque-Albelo <i>et al.</i> 2000
Pinzón	Crater	1984	Abedrabbo 1994
San Cristóbal	El Chino, La Lobería, El Progreso, Puerto Baquerizo Moreno, La Toma	1972	Silberglied 1972
Santa Cruz	Antiguo Basurero, Basurero Municipal, Bellavista, El Camote, El Cascajo, Cerro Ballena, Cerro Casifeo, Cerro Colorado, Cerro Crocker, Cerro Dragón, Cerro Maternidad, Cerro Mesa, Cerro Montura, Cerro Pastizal, El Chato, El Garrapatero, Los Gemelos, Mina de Granillo Rojo, Media Luna, Puerto Ayora, Santa Rosa	1905	Silberglied 1972
Santa Fe	None specified	1986	CDRS
Santiago	Los Guayabillos, James Bay, El Mirador, Punta Espumilla, La Trágica	1967	Lubin 1984
North Seymour	None specified	1998	CDRS

The record of *S. geminata* in La Caleta, Santa Fe in 1986 requires confirmation as it was not collected during two surveys in 2000 and 2003 (A. Mieles pers. comm., L. Roque-Albelo, pers. comm.). It is possible that it was eradicated from this area during a campaign to eradicate *W. auropunctata* in the early 1990s (Abedrabbo 1994).

W. auropunctata on Española could pose a threat to the Waved Albatross *Diomedea irrorata* Salvin, since *W. auropunctata* is known to affect the nesting behaviour of birds and reptiles (Roque & Causton 1999, Jourdan *et al.* 2001). The presence of *W. auropunctata* on islets is no less worrying as it has been shown to populate entire small islands and could affect other invertebrates that occupy these areas, in addition to nesting birds. Eradication programmes using Amdro (Hydramethylnon) have been effective against *W. auropunctata* on Marchena and Santa Fe islands in Galapagos (Abedrabbo 1994, Causton *et al.* 2005) and these methods could be applied to these new infestations.

RECOMMENDATIONS

Although ants are known to be among the most invasive insects, few studies have been carried out on them in Galapagos, limiting the ability of the Galapagos National Park Service to make management decisions. An inventory of ants should be conducted, especially in areas that are frequented by humans and that are lacking data, such as Baltra islet (military base) and tourist visitor sites, as well as conservation areas that are most vulnerable to invasive species (Santa Fe, Fernandina, Darwin, Wolf and smaller islands). Other entomological collections that house Galapagos specimens should also be reviewed to

establish a baseline for the native and introduced myrmecofauna.

In addition, the distribution of fire ants should be investigated in high priority areas such as nesting areas of threatened species such as the Mangrove Finch *Camarhynchus heliobates* (Snodgrass & Heller), and relatively pristine areas such as Wolf Volcano on Isabela.

Lastly, records of distributional data are important frames of reference (especially aggregated over time) for judging the significance of further incursions or changes in the distribution of invasive ant species. We therefore encourage other practitioners to publish data or submit data to the CDRS in order to build up the databases on these species.

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TWO BIRD RECORDS OF NOTE IN GALAPAGOS IN MAY 2006

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SUMMARY

The seventh records in Galapagos of Parkinson's Petrel *Procellaria parkinsoni* and of Pectoral Sandpiper *Calidris melanotos* are described.

RESUMEN

Dos notables registros de aves en Galápagos en mayo 2006. Se presentan el séptimo registro en Galápagos tanto del Petrel de Parkinson *Procellaria parkinsoni* como del Playero Pectoral *Calidris melanotos*.

PARKINSON'S PETREL

During the afternoon of 13 May 2006, between Floreana and Isabela at 1°10' S, 90°45' W, I saw three large, wholly dark-brown petrels sitting on the sea facing me, only c. 30 m away, with a hunched attitude as though "looking down their noses". Their only conspicuous feature was the white basal part of the bill. Alistair Duncan checked these features before the birds flew languidly away from us, showing us as they did so their all-black legs.

Swash & Still (2005) include a photograph matching these birds, of Parkinson's Petrel *Procellaria parkinsoni*. The similar Westland Petrel *P. westlandica* was ruled out by size: Parkinson's Petrel is about the same size (wing 350 mm, weight 682–778 g) as Fulmar *Fulmarus glacialis* (330 mm, 730–1000 g), a species I know well, whereas Westland Petrel is larger (385 mm, 1117–1294 g) (Cramp & Simmons 1977, Marchant & Higgins 1990). Westland Petrel is also unlikely to occur in Galapagos waters whereas Parkinson's Petrel is known to disperse from its breeding grounds off New Zealand as far as offshore from mainland Ecuador (Ridgely & Greenfield 2001).

Apart from Parkinson's and Westland Petrels, only one other comparably-sized seabird shows a similar white area at the base of the bill: Flesh-footed Shearwater *Puffinus carneipes*. However, our birds were clearly not shearwaters. *P. carneipes* also has pale legs.

It appears that our three birds could only be Parkinson's Petrels. This is the seventh record of the species in Galapagos waters; five of the six previous records were of single birds (Oct 1905, May and Jun 1906, Apr 2001, Aug 2004) while the other was a party of 15 in Aug 1977 (Wiedenfeld 2006). It appears that the species may be regular in Galapagos waters, as off Pacific Colombia (Estela *et al.* 2007).

PECTORAL SANDPIPER

On the morning of 14 May 2006, at Punta Moreno, W Isabela, A. Duncan spotted a wader on a lagoon, c. 70 m away. From its size, shape, leg colour and sharply defined

pectoral band I identified it as a Pectoral Sandpiper *Calidris melanotos*. After a few minutes it flew off giving the characteristic *trrt-trrt* flight call.

It was somewhat larger than a Dunlin *C. alpina* but unlike that species in shape. The upperparts were dark brown with prominent pale edges to the feathers, giving a scalloped appearance. The crown was streaked brown above a prominent cream supercilium, the breast heavily streaked dull brown with a sharp demarcation between the streaking and the rest of the underparts, which were pure white. This band came to a downward point in the centre of the lower breast. The bill was of similar length to that of a Dunlin but slightly down-curved throughout rather than primarily towards the tip. The legs were longer than in Dunlin and yellowish green. In flight, the dark-centred rump flanked by two prominent oval, white patches was conspicuous.

This appears to be the seventh record of this species in Galapagos, although some of the previous records are not supported by documentary evidence. Five of the previous records were of single birds while the other was of two together on San Cristóbal in November 1997 (Wiedenfeld 2006).

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NEW RECORDS OF INTRODUCED ANTS (HYMENOPTERA; FORMICIDAE) IN THE GALAPAGOS ISLANDS

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SUMMARY

Recent collections on Santa Cruz island and review of the Reference Collection of Terrestrial Invertebrates of the Charles Darwin Research Station, found five new records of ant species (Hymenoptera: Formicidae) possibly introduced to the Galapagos Islands: *Brachymyrmex heeri*, *Adelomyrmex myops*, *Cyphomyrmex rimosus*, *Pyramica membranifera* and *Rogeria curvipubens*. Four of these are also new records for Ecuador.

RESUMEN

Colectas recientes en la Isla Santa Cruz y revisión de la Colección de Referencia de Invertebrados Terrestres de la Estación Científica Charles Darwin, reportan cinco nuevos registros de hormigas (Hymenoptera: Formicidae) posiblemente introducidas para las islas Galápagos: *Brachymyrmex heeri*, *Adelomyrmex myops*, *Cyphomyrmex rimosus*, *Pyramica membranifera* y *Rogeria curvipubens*. Cuatro de estos registros también son nuevos para el Ecuador.

INTRODUCTION

The Galapagos Islands, 1000 km off the coast of Ecuador, have an ant fauna with a high proportion of introduced species (Wheeler 1919, 1924, 1933, Clark *et al.* 1982, Lubin 1984, 1985, Pezzatti *et al.* 1998, H.H. unpubl. data). As part of an ant survey, several new records are reported here.

METHODS

Material from collections on Santa Cruz island and material in the Reference Collection of Terrestrial Invertebrates of the Charles Darwin Research Station, Galapagos, Ecuador (IC CDRS) was examined in June 2005. The determination of the new records for Galapagos are based on Wheeler (1919, 1924, 1933), Kempf (1972), Clark *et al.* (1982), Lubin (1984, 1985), Brandão (1991), Pezzatti *et al.* (1998), Fernández & Sendoya (2004), Aesch & Cherix (2005) and Aesch (2006). The identified material was deposited in IC CDRS and the J.T. Longino Collection, Evergreen State College, Olympia WA, U.S.A. (JTLC).

RESULTS

Subfamily Formicinae

Brachymyrmex heeri Forel, 1874. Santa Cruz: 13 workers (Fig. 1), Puerto Ayora, Cancha de Squash, 25 Jan 2001 (M. Soria) [IC CDRS, JTLC]. The first record for Galapagos and continental Ecuador; widely reported from Central and South America and the Antilles (Kempf 1972). *Brachymyrmex heeri* is common in disturbed areas and has been introduced to many regions. In Galapagos, workers were attracted to honeydew produced by the introduced



Figure 1. *Brachymyrmex heeri* worker.

hemipteran *Icerya purchasi* Maskell. The species has also been collected in the agricultural zone of San Cristóbal island and urban zone of Isabela island.

Subfamily Myrmicinae

***Adelomyrmex myops* (Wheeler 1910)**. Isabela: one worker (Fig. 2) and one female, Cerro Verde, Agricultural Zone, 7 Jan 2003, Berlese (M. Lincango, A. Mieles) [ICCDRS]. First record for Galapagos. Not recorded elsewhere in (continental) Ecuador. Previously known from the lowlands of Guatemala, Honduras, Costa Rica, Panama and Colombia (Kempf 1972, Fernández 2003). There are no records of *Adelomyrmex myops* being introduced elsewhere. Its distribution and impact in Galapagos are not known. It is possible that *Adelomyrmex myops* occurred in Galapagos prior to human arrival, but was not reported before due to under-sampling. Additional Berlese or Winkler sampling throughout the islands may reveal more about its status as introduced versus native.

***Cyphomyrmex rimosus* (Spinola 1853)**. Light form: Santa Cruz: two workers (Fig. 3), Mina de Granillo Rojo, 580 m. 23 Jul 2001, pitfall (H. Herrera, P. Pozo) [ICCDRS]. Dark form: Santa Cruz: eight workers (Fig. 4), Km 4, Puerto

Ayora, casa de L. Roque-Albelo & V. Cruz (in Transition Zone, *sensu* Wiggins & Porter 1971), 4 Aug 2005 (L. Roque) [ICCDRS, JTLC]. The *C. rimosus* complex is widespread in the Neotropics, from the southern U.S.A. to northern Argentina. In some cases local communities appear to contain multiple sympatric forms, as in Florida, where a native form (*C. minutus*) is sympatric with an introduced form, the darker *C. rimosus fuscus* from southern South America. This also appears to be the case in Galapagos. The light form has also been collected from the agricultural zone of Isabela island. On Santa Cruz, workers of the dark form were found transporting leaves of *Cynodon dactylon* (L.) Pers., an introduced grass. On this island, nests of the light and dark form of *Cyphomyrmex* have been collected in areas dominated by the aggressive introduced species *Wasmannia auropunctata* Roger and *Solenopsis geminata* (F.).
***Pyramica membranifera* (Emery 1869)**. Isabela: one female (Fig. 5), Alcedo Volcano, high arid zone, 21–24 Apr 1998, Winkler (L. Roque) [ICCDRS]. First record for Galapagos. Not recorded elsewhere in (continental) Ecuador. Widely



Figure 2. *Adelomyrmex myops* worker.



Figure 3. *Cyphomyrmex rimosus* (light form) worker.



Figure 4. *Cyphomyrmex rimosus* (dark form) worker.



Figure 5. *Pyramica membranifera* female.

introduced to other tropical locations, including throughout the Caribbean and Florida (Kempf 1972). In the Galapagos it is recorded only on Isabela island. Its impact, and its distribution in the rest of the archipelago, are unknown.

***Rogeria curvipubens* Emery 1894.** Santa Cruz: two workers (Fig. 6), Bellavista, 180 m., 0°41'38.1''S, 90°19'16.8''W, 15 Jul 2005, Pooter (H. Herrera, #HWH 135) [IC CDRS, JTLC]. First record for Galapagos. Not recorded elsewhere in (continental) Ecuador. It is known from St Thomas, Cuba, Bahamas, Guyana, Bolivia (Kempf 1972) and Argentina (Fernández & Sendoya 2004). This species was collected in leaf litter in the agricultural zone. Its impact and distribution in the archipelago are unknown.

DISCUSSION

Although the impact of introduced species on island faunas is difficult to predict, none of these species are among those known to be pest ants or otherwise high-impact invasive species elsewhere. *Adelomyrmex myops*, *Pyramica membranifera* and *Rogeria curvipubens* are cryptic elements of

the leaf litter fauna, not reaching high densities and generally going unnoticed. *Brachymyrmex heeri* is tiny but is a more noticeable epigeic forager and can become locally abundant. It is not aggressive at resources and would not be expected to be a major threat to native species. However, impacts cannot be ruled out, especially when considering an island fauna. Finally, *Cyphomyrmex* forage for caterpillar droppings and dead insect parts, on which they cultivate a fungus for food. They can reach moderate abundances but are not aggressive or highly conspicuous. They are unlikely to have broad impacts on the native biota but could perhaps have an influence on the native *C. nesiotus* through competition.

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Figure 6. *Rogeria curvipubens* worker.

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ACTIVITY PATTERNS AND DISTRIBUTION OF GALAPAGOS BATS

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SUMMARY

Preliminary studies were carried out on the activity and distribution of the two species of Galapagos bat using heterodyne bat detectors. Monitoring at four sites on Santa Cruz Island from November 2003 to August 2005 revealed no evidence for seasonal migration between the highlands and lowlands for either species. Bat activity was lowest at all sites during December–March and increased over the year. The Hoary Bat *Lasiurus cinereus* was the commoner of the two species and showed three nightly activity peaks, as determined by all-night monitoring at one site in Santa Cruz Island over a period of three months in 2004. The Red Bat *Lasiurus borealis brachyotis* was common at only one site, El Cascajo village. Opportunistic monitoring throughout the archipelago over the study period confirmed the presence of the Red Bat on Floreana and revealed both species on Fernandina Island, a new island record for both. A new hypothesis is proposed, of seasonal migration between islands within the archipelago.

RESUMEN

Patrones de actividad y distribución de murciélagos de Galápagos. Se llevó a cabo estudios preliminares sobre la actividad y distribución de dos especies de murciélago de Galápagos usando detectores ultrasónicos. El monitoreo en cuatro sitios de la Isla Santa Cruz, realizado entre noviembre de 2003 y agosto de 2005, no reveló evidencia de migración estacional entre las tierras altas y las costas, para ninguna de las especies. La actividad de los murciélagos fue la mínima en todos los sitios durante los meses de diciembre a marzo y se incrementó a lo largo del año. *Lasiurus cinereus* fue la más común de las dos especies y mostró tres picos de actividad durante la noche, como fue determinado por monitoreos que duraron toda la noche en uno de los sitios en Santa Cruz, que fueron efectuados durante un periodo de tres meses del año 2004. *Lasiurus borealis brachyotis* fue común solo en uno de los sitios, la villa El Cascajo. Monitoreo ocasional a lo largo del archipiélago durante el periodo del estudio confirmó la presencia de *L. borealis* en Floreana, y la aparición de las dos especies en la Isla Fernandina, lo que representa un nuevo registro en esta isla para ambas. Se propone una nueva hipótesis: una migración estacional entre islas dentro del archipiélago.

INTRODUCTION

The Galapagos archipelago has few native mammals. Only two species of bat occur, the native Hoary Bat *Lasiurus cinereus* and the endemic subspecies of the Red Bat *L. borealis brachyotis* (Koopman & McCracken 1998). Apart from a few anecdotal references, only one study has been undertaken on the bats to date, in 1990 and 1991 on the five islands Santa Cruz, San Cristóbal, Isabela, Floreana and Santiago (McCracken *et al.* 1997, Koopman & McCracken 1998, Whitaker & McCracken 2001).

McCracken *et al.* (1997) found that the Hoary Bat was present on all five islands, while the Red Bat was present on only Santa Cruz and San Cristóbal, although previous records suggest it had been present on Floreana in the past (Steadman 1986). Both species forage around street lights at night in the inhabited areas, and appear to be more common in the lowlands during the months of July to December, and in the highlands in the period January to June (McCracken *et al.* 1997). As McCracken's work was undertaken during the months of June to August, these findings are tentative. McCracken postulated a seasonal

migration of bats from the highlands to the lowlands in July–December, with anecdotal evidence that breeding takes place in the highlands during January–June (Brosset 1963 cited by McCracken *et al.* 1997). McCracken was unable to detect any breeding activity during his two studies.

With the aim of extending McCracken's work, three studies on the activity and distribution of the two species of bat in the archipelago were carried out from 2003 to 2005 to address three questions:

1. Is there any evidence to support the hypothesis of seasonal migration between the highlands and lowlands?
2. Do Galapagos bats show distinct activity patterns over the night?
3. How widespread are they within the archipelago?

In order to answer the first question, a long-term monitoring study was carried out in the highlands and lowlands on one island (Santa Cruz) from November 2003 to August 2005, to see if bat activity levels vary from site to site over the year or remain constant. For the second, all-night monitoring was carried out at one site over a 3-

month period in 2004. The third question was partially answered through opportunistic monitoring carried out throughout the archipelago whenever possible.

METHODS

Monitoring

For all three studies, bats were monitored using hand-held heterodyne ultrasonic bat detectors (Bat Box 3 and Petersen Ultrasound Detector D 200), which convert the ultrasonic cries of bats to a frequency detectable by the human ear. The two species can be readily distinguished on the basis of both the frequency of their calls and their pattern of flight (McCracken *et al.* 1997, pers. obs.), with Hoary Bat calling at 25 kHz, and direct flight, high above street lights, and Red Bat calling at 45 kHz, with fluttering flight, below streetlights. Monitoring was not carried out in heavy rain as bat activity in these conditions is known to be minimal (McCracken *et al.* 1997 and pers. obs.).

Long-term monitoring. Four sites on Santa Cruz Island were routinely monitored (Fig. 1), aiming to sample bat activity at each at least once for each month of the year. The nightly activity patterns of Galapagos bats were not known at the initiation of this study and so a relatively narrow time period was defined during which all monitoring was carried out to minimize the risk of bias: between 18h30 and 21h30. At each sampling visit, bat activity was assessed by the number of bat passes recorded over two 5-minute periods each night, one with the detector tuned to the Hoary Bat (25 kHz), and one tuned to the Red Bat (45 kHz). The order of recording (*i.e.* Red Bat first or Hoary Bat first) was alternated at each monitoring session. A bat pass is defined as the sound of an individual bat passing the observer within the range of the bat detector. The number of feeding buzzes was also recorded for each species during each monitoring period.

All-night monitoring. Nine sites were selected in Puerto Ayora town and monitoring was carried out using the

protocol described above, covering all the 1-h periods from dusk to dawn, 18h00–5h30, during the period February–May 2004. A single site and limited time period were used to avoid the complication of seasonal and site effects.

Opportunistic monitoring. For the towns and agricultural zones of San Cristóbal, Floreana and Isabela islands, several monitoring visits were carried out using the long-term monitoring protocol described above. For uninhabited areas on these islands, and other uninhabited islands, in most cases only a single visit was possible and monitoring was done for a longer period, switching frequency irregularly over periods of 20 minutes to several hours, in order to establish the presence of any bats at the site.

Study sites

Both the long-term and all-night monitoring studies were carried out on Santa Cruz Island, the second largest island in the archipelago (986 km², elevation 834 m). A preliminary survey along the entire island road system (outside Puerto Ayora) was conducted in Oct–Nov 2003 using the protocol described above. Both species showed relatively high levels of activity around street lights and relatively low levels in unlit areas. Routine monitoring sites were therefore established near street-lit areas in order to maximise the potential data collected.

The four sites selected for the long-term monitoring represent lowland (dry), highland (wet) and intermediate (wetter and drier) zones:

1. Lowland (dry): Puerto Ayora town, 30 m a.s.l.
2. Intermediate (relatively wet): Bellavista village, 190 m a.s.l., within the Transition vegetation zone of Wiggins & Porter (1971).
3. Intermediate (relatively dry): El Cascajo village, 250 m a.s.l., at the eastern, drier end of the agricultural zone, within the Transition vegetation zone.
4. Highland (wet): Santa Rosa village, 400 m a.s.l., in the upper Transition or lower Scalesia vegetation zones.

The all-night monitoring study was carried out in 2004 at nine well-lit sites, at least 250 m apart, around the outskirts of Puerto Ayora town.

Data analysis

To examine the hypothesis of seasonal migration, seasons were defined by examination of the temperature and rainfall data for the three years of the study at the two weather stations maintained in Puerto Ayora and Bellavista by the Charles Darwin Research Station. Monthly temperatures varied relatively little over the study period, with a maximum recorded temperature of 26.4°C in March 2003 and minimum of 19.2°C in August 2004 (range of 7.2°C over the three years). These temperature variations are not considered critical for *Lasiurus* species and so were not considered further. Rainfall affects bats directly, and indirectly by affecting their main food source, insects. Average monthly rainfall figures for

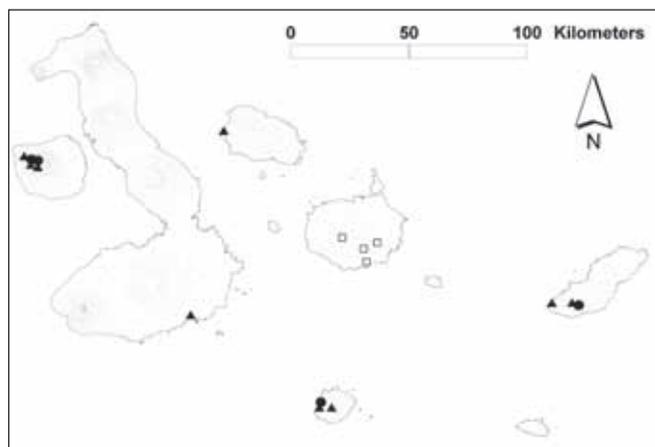


Figure 1. Monitoring sites on Santa Cruz (squares), and sites where Red Bats (circles) and Hoary Bats (triangles) were detected on islands other than Santa Cruz.

Puerto Ayora and Bellavista (Fig. 2) suggest grouping into three seasons: 1 = wet (Dec–Mar), 2 = dry (Apr–Jul), 3 = transition (Aug–Nov). The all-night monitoring data were collected during Season 2 in 2004.

RESULTS

Long-term monitoring

Altogether, 406 distinct 5-minute sampling periods were recorded for Hoary Bat activity, and 391 for Red Bat activity (Table 1). There is heavy weighting of data collection to Puerto Ayora and Season 2 for logistical reasons. There was a significant positive correlation between the number of feeding buzzes and passes for both Hoary Bat ($r = 0.598$, $df = 405$, $P < 0.001$) and Red Bat ($r = 0.694$, $df = 390$, $P < 0.001$).

There was no evidence that Hoary Bat activity changed site according to the season (Fig. 3). Hoary Bat activity was lowest at all sites in Season 1, showing an overall increase over Seasons 2 and 3 with distinct peaks of activity in Season 3 in Bellavista and Santa Rosa; the peak occurred in Seasons 2 and 3 at El Cascajo.

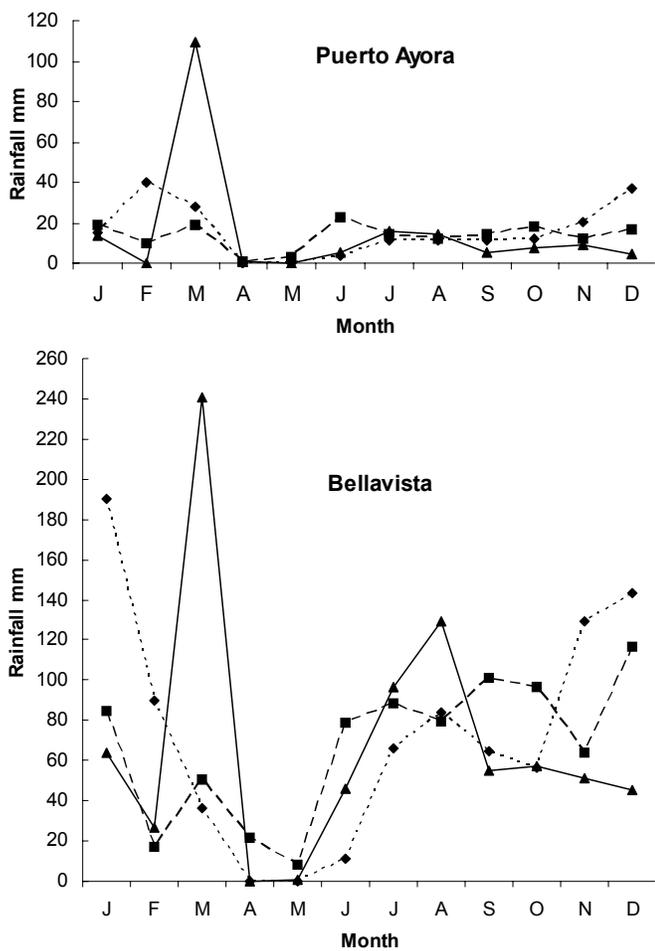


Figure 2. Monthly average rainfall at Puerto Ayora and Bellavista for 2003 (diamonds), 2004 (squares) and 2005 (triangles).

Table 1. Sampling occasions for the Hoary Bat (HB) and Red Bat (RB) by site and season.

	Season 1		Season 2		Season 3	
	HB	RB	HB	RB	HB	RB
Puerto Ayora	92	94	94	89	19	19
Bellavista	16	16	23	22	14	8
El Cascajo	16	16	33	31	12	12
Santa Rosa	20	20	53	50	14	14

There was also no evidence that the Red Bat changed site according to season (Fig. 4). Its activity was lowest at all sites in Season 1, with slight peaks of activity in Season 2 in Puerto Ayora and Bellavista, and a sharp peak in Season 3 in Santa Rosa. The Red Bat was common at only one site, El Cascajo.

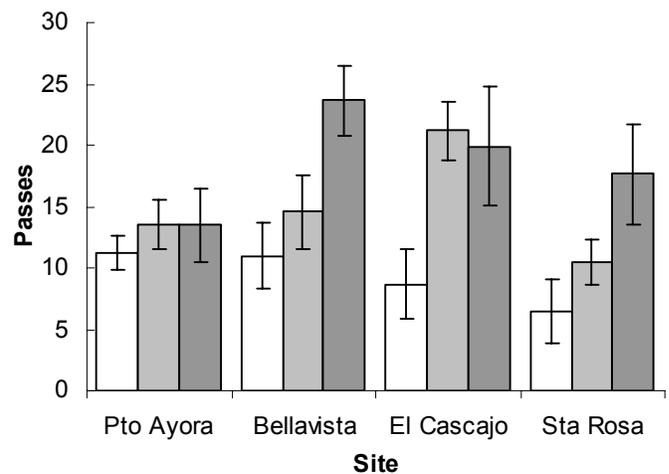


Figure 3. Average (±1 S.E.) number of Hoary Bat passes for four long-term monitoring sites on Santa Cruz during the three seasons.

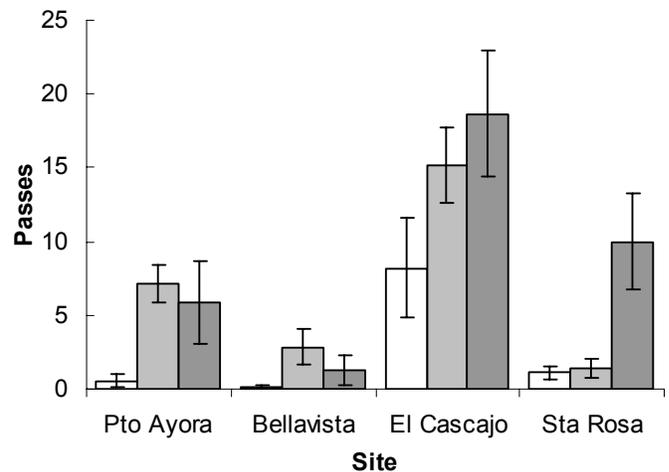


Figure 4. Average (±1 S.E.) number of Red Bat passes for four long-term monitoring sites on Santa Cruz during the three seasons.

Table 2. Sampling periods for the Hoary Bat during each hour of the night, from 18h00 to 6h00.

Hour beginning:	18h00	19h00	20h00	21h00	22h00	23h00	0h00	1h00	2h00	3h00	4h00	5h00
Number of sampling periods	26	45	54	46	40	36	45	35	24	27	29	28

Nocturnal activity patterns

Sufficient data for analysis are only available for the Hoary Bat as Red Bat activity was relatively low. A total of 435 distinct 5-minute sampling periods were recorded for Hoary Bat activity (Table 2).

Hoary Bats were active all night long, and there was no time when activity was not detected (Fig. 5). Three peaks of activity can be discerned: 19h00–20h00, 24h00–1h00, and 3h00–4h00. There was no evidence that the Hoary Bat emerged before dusk or remained active after dawn, as the two lowest periods of activity are around

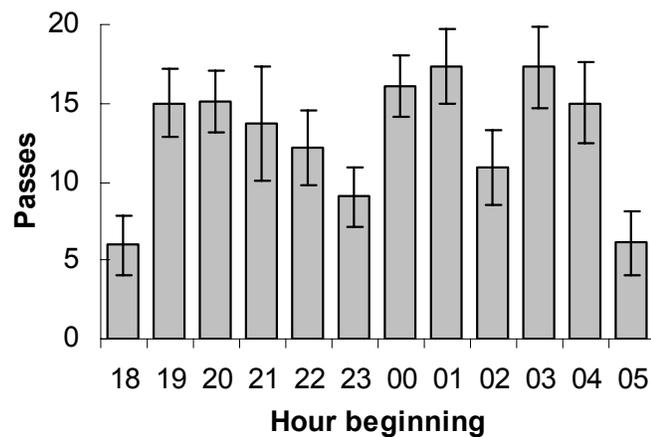


Figure 5. Average (±1 S.E.) number of Hoary Bat passes from 18h00 to 6h00, in Puerto Ayora during Season 2.

these times, 18h00 and 5h00 and bats were not seen during full daylight.

Bat presence on other islands

Surveying was carried out opportunistically on eight other islands (Table 3). The Hoary Bat was detected on five islands in addition to Santa Cruz: Isabela, San Cristóbal, Floreana, Fernandina (both the crater rim and slope) and Santiago (Fig. 1). The Red Bat was found on three islands in addition to Santa Cruz: San Cristóbal, Floreana and Fernandina (slope and rim) (Fig. 1). Fernandina Island is a new distribution record for both bat species.

These results in most cases reflect a single monitoring event; repeated monitoring visits took place only on San Cristóbal. Consequently a failure to detect a species does not necessarily mean that it does not occur there.

DISCUSSION

No evidence of seasonal migration between the four sites monitored on Santa Cruz Island was found for either species. For both, activity was lowest at all sites in Season 1 and overall highest in Season 3, as found by McCracken *et al.* (1997) in 1990 and 1991. However, both *Lasiurus cinereus* and *L. borealis* are known to exhibit distinct seasonal and sexual geographical distribution in the U.S.A. (Caire *et al.* 1986, 1988, McCracken *et al.* 1997), with males and females occurring at different sites. This was an aspect of the

Table 3. Results of surveys for Hoary Bat and Red Bat on islands other than Santa Cruz.

Island	Site	Date	Total minutes monitored	Hoary Bat detected	Red Bat detected
Isabela	Agricultural zone	Mar 2004	20	No	No
	Coastal town	Mar 2004	20	Yes	No
San Cristóbal	Agricultural zone	Intermittent over the year		Yes	Yes
	Coastal town	Intermittent over the year		Yes	No
Floreana	Agricultural zone	Apr 2004	20	Yes	No
	Coastal town	Apr 2004	20	Yes	Yes
Pinzón	Plateau (0°36'40.5''S, 90°40'11.5''W)	Jan 2005	60	No	No
Rábida	Visitor site (0°24'0.6''S, 90°42'25.2''W)	Jan 2005	60	No	No
Fernandina	NW rim of crater	Nov 2004	not recorded	Yes	Yes
		Feb 2005	105	Yes	No
	Cabo Douglas (0°18'15.9''S, 91°39'3.7''W)	Feb 2005	90	No	No
	Ascent Camp 1 (0°20'30.2''S, 91°36'58.2''W)	Feb 2005	90	Yes	No
	Ascent Camp 2 (0°21'16.3''S, 91°35'20.8''W)	Feb 2005	190	Yes	Yes
Santiago	Puerto Egas	Mar 2005	165	Yes	No
Española	Gardner Bay	Jun 2005	60	No	No

behavioural ecology of these species not studied here. Further, the data reflect overall bat activity levels, not bat numbers or individual identity, which may obscure actual distribution differences.

The Hoary Bat was the most common species and was found at all sites monitored on Santa Cruz and in all months, although it is not conspicuous due to its habit of flying fast and high, above the street lights. The Hoary Bat is generally considered a robust species, occurring across the Americas from the U.S.A. to Chile. It is now recorded from six islands in the archipelago, with a new record for Fernandina.

The Red Bat has a more restricted distribution in the Americas and is much less well known. It is now known from four islands in Galapagos; its suspected presence on Floreana has been confirmed and there is a new record for Fernandina Island. Overall this species had lower activity levels than the Hoary Bat and is almost completely absent from Puerto Ayora, Bellavista and Santa Rosa in Season 1 (Dec–Mar). The only site where it was consistently observed was El Cascajo, a small village at the driest, eastern end of the agricultural zone, with increasing activity over the year. During Season 1, searches were made along the cross-island road on Santa Cruz with the bat detector tuned to 45 kHz, but with no Red Bats detected. Three hypotheses are postulated for the change in Red Bat activity over the year: a change in foraging behaviour, *e.g.* between hawking insects around lights, and gleaning; a change in habitat use, *e.g.* moving into the National Park area; migration within the archipelago to other islands. Bats are typically flexible and adaptable in their foraging strategies (Fenton 1990) so seasonal changes would not be surprising, probably linked to prey abundance and availability rather than climate directly. As noted by McCracken *et al.* (1997) Red Bats are migratory in other parts of their range, over distances greater than those between the different Galapagos Islands. The hypothesis of seasonal migration within the archipelago requires further investigation, especially for the Red Bat.

The Hoary Bat is typically considered a late flyer, appearing several hours after dusk, with an activity peak after emergence and then a second before dawn (Caire *et al.* 1986). The activity pattern found by this study was unclear, with bats active all night and possibly either two or three peaks suggested by the data (Fig. 5). A pattern

of three peaks with one around 3h00 is shown by *Mormops megalophylla* in Pichincha, Ecuador (Boada *et al.* 2003), and may be a feature of tropical bats. This requires further study.

This preliminary study has expanded our knowledge of the movements and distribution of the Galapagos bats, and has highlighted the need for further work to explore the distribution and movements of the two species within the archipelago, particularly the more elusive Red Bat.

ACKNOWLEDGMENTS

We would like to acknowledge the Galapagos National Park, which gave permission for this work, the Charles Darwin Foundation for support, Washington Tapia for advice and encouragement, Gary McCracken for advice and the loan of equipment, Solanda Rea for the meteorological data, and all the people who joined us at night and shared the loneliness of nocturnal bat monitoring.

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GUEST EDITORIAL

GALAPAGOS: PAST, PRESENT AND FUTURE

By: Graham Watkins & Andrea Marín

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Galapagos is an extraordinary and special place, and over the last 50 years, the Charles Darwin Foundation (CDF) has made substantial contributions to the conservation of the islands. In this edition of Galapagos Research, we take stock of the past and present, and look toward the future of the CDF.

The past work of the CDF has led to many successes in conserving endangered species and managing invasive species, the legacies of Galapagos's whaling and colonizing history. CDF has also supported the building of stronger local organizations including the Galapagos National Park and Galapagos Quarantine System. In addition, the CDF played a seminal role in the early development of tourism and in establishing the control of direct impacts through guides, trails and itineraries.

Despite the hard work of the past 50 years, Galapagos finds itself today at risk; the President of Ecuador and UNESCO both declared Galapagos as such in 2007. The last 20 years have seen rapid economic growth, unregulated development, and alarmingly rapid immigration. This has brought about rapid political, social and cultural change, with an increasing population and new migrants bringing a heterogeneous culture from the mainland. These changes have increased the risks of the arrival of introduced species in cargo boats, planes and tour boats, and some of these species have proven to be complex conservation challenges.

The future CDF will need to be equipped to deal with these and other changes still to come. CDF will need to work collaboratively with government agencies to provide innovative solutions to these challenges. CDF will also need to work with the local community and

their representatives to help build a sustainable society. Included among these challenges will be the need to create an integrated research and monitoring framework to guide effective decision-making.

During 2009, the CDF will celebrate 50 years of its existence. During 2007, the Galapagos Islands were declared at risk because of the changes they have seen over the last 20 years. The CDF will need to change its role in Galapagos to address the challenges of today and the future, based on the lessons from the past. The Galapagos Islands are unique; to lose them or see them degrade further would be a terrible loss for humanity. The CDF of today and the future needs to work with all interested parties to support a shared view of the islands and so help develop a shared vision for the future.

The articles in the following special Galapagos Commentary stem from talks presented at a symposium held at the CDF General Assembly meeting in November 2007. Their authors review aspects of the past, present and future of the CDF and Galapagos conservation, and suggest directions for the critical role that the CDF will play in determining the future of these extraordinary islands.

ACKNOWLEDGMENTS

CDF extends thanks to the following for financial support for the symposium at which the papers in the following section were originally presented: Ecuador's National Council for Higher Education (CONESUP) and National Secretariat for Science and Technology (SENACYT), the Galapagos Conservancy, IUCN and UNESCO.

GALAPAGOS COMMENTARY

AN INCONVENIENT TRUTH AND SOME UNCOMFORTABLE DECISIONS CONCERNING TOURISM IN GALAPAGOS

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SUMMARY

The truth is that limits must be placed on growth in Galapagos, in order to achieve sustainability. I discuss the recent and projected growth in tourism to the islands and possible methods of achieving sustainability in the tourism industry, to make it compatible with the conservation of the islands. A move towards greater income per visitor, and tighter regulation of tourism linked to responsible operations and behaviour, are essential if sustainability is to be achieved.

RESUMEN

Una verdad inconveniente y decisiones incómodas acerca del turismo en Galápagos. La verdad es que debe imponerse límites al crecimiento económico en Galápagos para lograr su sostenibilidad. Analizo el crecimiento reciente y proyectado del turismo a las islas y posibles métodos para lograr sostenibilidad en el sector, para hacerlo compatible con la conservación de las islas. Un cambio hacia un mayor ingreso por visitante, y una reglamentación más estricta del turismo vinculada a operaciones y comportamiento más responsables, son imprescindibles para lograr la sostenibilidad.

THE TRUTH

The truth is that if we want sustainability, we have to place limits on ourselves. The issues in Galapagos are uncomfortable to deal with and we put off their analysis and solution because the measures that must be taken, in the long run beneficial for everyone, threaten the individual short-term interests of us all.

Recently, a consultant for the World Bank, who had been commissioned to do a study on the situation in the Galapagos Islands, interviewed me and ended by posing the question “to sum up in just one sentence what the core problem in Galapagos is.” I answered “More is better.” I explained that the predominant global view is to qualify growth as good. In this ethic, we do not consider the expense at which this growth is produced. It matters little in this view if the growth in the economy degrades natural resources or negatively affects the health, equity or dignity of a populace.

This globally common view is widely accepted by Ecuadorians who are involved with Galapagos. Thus, the fishing sector will be “better” this year if more fish are caught than last year. The government bureaucracy will feel that it is “progressing” if the state spends more money and can employ more people. The tourism sector will feel that it is on the right track if it manages to increase the

tourist flow, and the scientific sector will be happy if it has more researchers and does more studies. All the stakeholders are subject to, and often unwitting proponents of, the paradigm of growth: if we grow, we are progressing; if we stop growing, grow at a reduced rate or worse, shrink, we are losing ground. Nevertheless, in a place as isolated, unique and finite as the Galapagos Archipelago, we cannot apply this paradigm and hope to maintain our resource base. We can only guarantee sustainability if a limit is set on growth.

In many Galapagos development plans, the word “sustainability” is bandied about very lightly, with little thought to four basic principles on which it depends:

1. that natural resources are limited;
2. that we have to set limits for ourselves;
3. that resource use be responsible and lasting; that is, that it endure throughout time, such that the benefits derived by current generations do not come at the expense of lost opportunities for future generation;
4. that there be a union of interest and purpose among stakeholders, who must be committed to sharing the resources, life and culture of a place with the rest of the planet and its inhabitants.

Of these principles, the first is the one that requires that the others be followed.

Thus, the uncomfortable truth is that if we want the intrinsic values of Galapagos to last forever, we must make responsible use of its resources, sharing the benefits with all stakeholders; and this starts with the voluntary or enforced establishment of a limit on growth.

TOURISM, THE MECHANISM THAT GENERATES GROWTH

Growth in tourism became exceptional after the end of the Second World War because of the postwar economic boom and the improvement of transportation, especially sea and air travel. In 1950, there were less than 30 million tourists each year worldwide. Sixty years later (2010), there will be one billion; the annual growth rate has ranged from 4 % to 7 %. Growth in NW South America is even more accelerated, due to extensive investment in promotion. In 2007, tourism to Colombia grew by 16.6 %, with a marketing investment of US\$36 million, Peru increased its tourist industry 9 % by investing US\$19 million, and Ecuador achieved 12 % growth by attracting more than 900,000 tourists through an investment of US\$6 million. Without doubt, at such high growth rates, the quality and status of heavily visited tourist destinations will deteriorate unless sustainability is cultivated.

The Ecuadorian government now plans to attract 1,500,000 tourists by 2010 and to invest US\$15 million in 2008 to promote tourism to the country. Galapagos is part of this trend, with growth averaging 16.8 % over the three years 2005–7. Using this rate to forecast the number of tourists arriving in Galapagos suggests that numbers will exceed 300,000 by 2011, or double the 2007 figure.

CURRENT CAPACITY, SATURATION AND INFORMATION NEEDS

Epler (2007) gives accommodation capacity on cruise ships and at hotels on the islands as 3493 berths and beds at the end of 2006, comprising 1805 berths on board 80 vessels offering cruises and 1688 beds in 66 hotels. The question is often asked, when will we end up using the full installed capacity? However, using 100 % of the installed capacity is almost impossible, for several reasons:

There is a growing trend in tourism to charge per room or cabin rather than per occupant. This is accompanied by an increasing flow of travellers who are not willing to share a room, which lowers the occupancy of hotels and ships but does not reduce income.

In general, cruise vessels achieve greater levels of occupancy than hotels because they control the entrance and departure of passengers on one particular day. Hotels often have a few days' vacancies because passengers can enter and leave the hotel on any day. Hotels depend on other services such as space on day-tour boats, so their appeal is limited by the availability of these; however, increased availability of such services could markedly

increase hotel occupancy. In general, demand for cruises is on the rise worldwide, while vacationing at hotels shows less growth.

On the other hand, hotels do not need to stop their operations for annual maintenance, whereas vessels have to dry dock, which forces them to suspend operations for four weeks each year on average. Thus, hotels can operate 365 days a year, while vessels are limited to around 336 days (48 weeks).

Finally, cruise vessel and hotel businesses are both subject to seasonal slumps when it is difficult to achieve high occupancy. These periods are the last week in May and the first in June, the last two weeks in September and the first two weeks in December.

The foregoing considerations suggest that maximum occupancy for vessels is in the 90 % range and that hotels achieve about 80 %.

As most ships operate one-week tours, with a 3–4 day tours also popular, and relatively few longer tours, an average stay may be taken to be c. 5 nights. Hotels get an average of three nights per visitor. Thus, the maximum number of visitors per year can be estimated as follows:

$$\begin{aligned} \text{Vessel capacity} \\ &= \frac{336 \text{ days} \times 1805 \text{ beds} \times 90 \% \text{ occupancy}}{5 \text{ night average}} \\ &= 109,166 \text{ visitors;} \end{aligned}$$

$$\begin{aligned} \text{Hotel capacity} \\ &= \frac{365 \text{ days} \times 1688 \text{ beds} \times 80 \% \text{ occupancy}}{3 \text{ night average}} \\ &= 164,298 \text{ visitors.} \end{aligned}$$

With the facilities recorded by Epler (2007) and the above estimates, Galapagos can handle a maximum of 273,464 tourists per year. This is almost double the number the number that arrived in 2006, but based on the above growth estimates, saturation of current facilities would take place in January 2011.

To handle demand beyond 2011, more hotels, restaurants and day-tour and cruise operating permits would be required. All this will require more: more electrical power, more food, more water, more fuel, and a larger workforce: and thus more immigration, more garbage, more transportation, more introduced species and greater danger to sustainability.

More significantly, the limited carrying capacity of visitor sites indicates that Galapagos cannot handle double the number of tourists projected to arrive in the next three years.

It is obvious that the uncomfortable truth that Galapagos cannot sustain such growth calls for two equally uncomfortable decisions: setting a limit on the number of tourists that can visit Galapagos annually.

To improve on the rough calculations above and get a more accurate idea of the magnitude of tour cruise operations, it is vital to continue to monitor each year the number of cruise passengers, as well as the average number of operating days, occupancy measured by the

number of passengers, and the average length of stay. Similar information is needed with respect to currently unregulated on-land hotel operations, which have seen explosive growth over the last five years and thus represent even greater cause for concern. We need to know total hotel capacity, including facilities in private residences, the number of operating days per year, average stay, use of tour boats, diving activity, bay tour statistics *etc.*

SETTING POLICIES AND LIMITS

Above all, the government should set up a strict tourism control authority. It will undoubtedly be necessary to adapt tourism development policies to the varying circumstances of each inhabited island. Puerto Ayora is on the verge of saturation, while Puerto Baquerizo Moreno has room for considerable tourism development, particularly in specialized areas such as non-polluting water sports. Puerto Villamil will require special consideration of the appealing concept of ecological tourism through local participation, which is being developed there. Something similar may occur in the case of Floreana.

There are several things to consider in accomplishing the awkward decision of setting a limit on the number of tourists who will be allowed to come to Galapagos. First, more accurate figures will clarify the trends and facilitate responsible decisions, so better information-gathering is required. Second, limits must be set for each activity and area so that the total number of authorized visitors is commensurate with the impacts of each activity, either land-based or cruise tourism. In particular, limits on land-based tourist activity must be apportioned by areas, to ensure compatibility with carrying capacities and to achieve balanced development. The limit must also be conservative and precautionary, and it should be revised only at rather long intervals, meaning every 20 years or so. This will enable evaluating the effectiveness of resource management to determine if resource quality is being maintained in accord with the principle of sustainability and whether higher limits can be allowed or not.

Consequences of setting limits

Positive results of setting limits which sacrifice growth for sustainability include the enhancement of Ecuador's global image. It will also contribute to the removal of Galapagos from the UNESCO list of World Heritage in Danger. There may also be increased demand from world tourism, because declaring a limit will create a scarcity syndrome that, in turn, will push up demand. Tourist service prices will also go up and operators will be able to reduce debt and enjoy earnings that enable them to renovate their infrastructure and improve their service quality. There will be increased willingness by visitors to pay the Galapagos National Park (GNP) entrance fee and by operators to pay license fees and duties, meaning greater income for all those who share in the fees. The greatest beneficiary will be the GNP, which will have

more resources for conservation and restoration, which, in turn, will give Galapagos greater distinction. The possible establishment of waiting lists will enable tour operators to lower their marketing costs by reducing promotional efforts, paying smaller commissions to international wholesalers, or using the internet to market products directly to travellers. Tourist spending will rise, since the average consumer will be from a higher income bracket. This will allow handicraft dealers and on-land suppliers of services ranging from food to adventure experiences, cultural and artistic events to command better prices for their goods and services, which, in turn, will promote better quality offerings.

On the other hand, negative outcomes include a reduced Galapagos contribution to tourist flow through continental Ecuador. Once the Galapagos limit has been reached, promotional efforts will have to be focused on continental tourism. A graver consequence is that the greatest beneficiaries will be those who possess operating licenses; everyone else will be marginally benefited or left out, including many people who have the necessary initiative and managerial ability to enter the primary tourism management business. This goes against sustainability principle 4, of solidarity and sharing. There may also be an increased cost of living for local people, and Galapagos may become out of reach for most Ecuadorian tourists, due to higher pricing for high-end tourists.

Addressing the negative consequences

Reversing these negative consequences will have to be addressed through supportive measures by licence holders, such as the following. First, all regulated tourism industry operators (hotels, cruise vessels, day tours, bay tours, cruise diving, day-trip diving, complementary operations *etc.*) should have to open their capital to permanent residents of Galapagos within a reasonable period of time, so that the portion of the population that is currently not directly involved in these activities can become stockholders and receive benefits from tourism. To this end, programmes for the sale of convertible preferred stock could be developed, with purchasing financed through national and international financial institutions.

Licensed operators should be prohibited from vertical integration. In other words, tour operators should not be able to have their own on-land passenger transport service or be direct producers of food for tourists. This will allow more citizens to benefit from tourism as suppliers, even if they are not direct tourism service providers. There should be a list of trained and capable people interested in going into the direct tourism business. These people would be given preference in acquiring a licence when an operator loses a licence through non-compliance or when a quota freeze period (*e.g.* 20 years) expires and authorities deem that tourism could be further expanded based on the status of resources and installed management capacity.

However, it is vital that preferential access to business shares or tourism operator permits and jobs should be made contingent on a set of agreed principles and practices to promote the local society becoming more attuned to the need for a community culture that recognizes and adopts limits to achieve sustainability. Simply providing more economic benefits to the local population, although politically correct and socially expedient, does nothing to promote sustainability and could result in greater problems as additional revenues within the current culture could finance unsustainable local development. To achieve sustainability, the provision of preferential access to benefits should be closely tied to increases social, corporate and personal responsibility.

Raising the GNP entrance fee is always controversial, because it may irk the operators, the wholesalers and the tourists (depending on perceived value for money) and generates ambitions on the part of those institutions that share in the revenues. Nevertheless, it must be done, in order to be able to finance the activities and infrastructure vital for the satisfactory functioning of Galapagos society and the conservation of the archipelago. The GNP is of incomparable importance as one of the best conserved of the world's archipelagos and national parks, despite UNESCO's declaration that it is in danger. It is logical, therefore, to charge a fee compatible with the quality of the destination. Today, foreign visitors are charged \$100 and Ecuadorians \$6, no matter the length of stay. If the average stay is 5 nights, then the daily cost is \$20 for foreign tourists and \$1.20 for nationals. This is far less than what is charged at world-class national parks whose importance does not match that of the GNP. Parks in Costa Rica (Cocos Island), Kenya, Tanzania and South Africa charge between \$30 and \$50 per day. It would be advisable to start by increasing the GNP entry fee for international visitors to \$30 per day, with a plan for increments over the next five years to reach \$50 per day. The cost to Ecuadorians should be computed based on ability and willingness to pay, but should also include incremental increases parallel to those applied to foreign visitors. There should be a concessionary price for children and senior citizens. An extra diving fee could also be set. Any change in rates will require sufficient advance notice (at least one year) so that already arranged tours will not be affected.

This decision depends on who the beneficiaries of these revenues will be and what accountability they must provide in terms of complying with explicit rules regarding how revenues can be spent, to ensure they are used for ends that do not undermine the goal of sustainability. There must also be a decision as to how the cost of collection and disbursement, currently undertaken by the GNP alone, is to be covered.

Resource potential from this process can be illustrated as follows (although the actual rates set should be based

Table 1. Potential income from an increased GNP entrance fee (for details of calculation see text).

Year	Total visitors	Ecuadorians	Foreigners	Total Income
2009	230,000	23,000	207,000	\$25.1 M
2010	269,000	27,000	242,000	\$34.2 M
2011	314,000	31,000	283,000	\$45.7 M
2012	366,000	37,000	329,000	\$59.8 M
2013	427,000	43,000	384,000	\$77.6 M

on a willingness-to-pay study). Assuming that 20 % of revenues will come from Ecuadorian citizens with an average stay of 4 nights and who pay 10 % of the amount paid by foreign visitors, and that no limit on total tourist numbers is fixed up through the year 2013 (which in my opinion would be absurd), future revenues from fees could be as in Table 1. We can conclude that such revenues could provide for the whole population of Galapagos in the near future. If the population were stabilized in the next six years at 30,000 inhabitants, the rates would represent a per capita annual income of US\$2586 by 2013.

This income would not only improve the political climate for conservation of the GNP, assuming that the funds were spent in ways that compatible with conservation goals, but could also be used to provide for alternative energy sources, high-quality drinking water, sewage and solid waste management, prime-quality education, first-class health services, suitable infrastructure, and investments in culture and sports, all of which would not only provide identity and pride to a content populace, but would be an example of good governance. However, as mentioned above, the generation of benefits must be linked to commitment by the local populace to limit itself in terms of lifestyle choices. Increased revenues should be used to create an island identity consistent with the unique qualities and fragility of Galapagos. Otherwise, there will simply be more cars, larger air-conditioned houses requiring more energy, more garbage produced, more pedigree pets that eventually run feral *etc.* Increased funding alone could exacerbate, rather than solve problems if not linked to environmental responsibility.

The issues put forth in this paper are complex and require a deeper analysis, however we are running short of time and must take these decisions now, courageously and conscientiously. It is time to act.

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A PARADIGM SHIFT IN GALAPAGOS RESEARCH

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SUMMARY

The Galapagos Islands are under threat. I argue that social sciences in Galapagos must be strengthened so as to improve management, and that Galapagos must be seen as a social and ecological system rather than as an ecological system in which people are considered adjuncts.

RESUMEN

Un cambio de paradigma en la investigación de Galápagos. Las Islas Galápagos están bajo amenaza. Sugiero que las ciencias sociales en Galápagos deben ser fortalecidas para mejorar las estrategias de manejo, y que Galápagos debe ser considerado como un sistema ecológico y social en lugar de un sistema ecológico en el cual la gente es considerada como un aspecto complementario.

INTRODUCTION

The Galapagos Islands appear in the international news as “in crisis,” “under threat,” and “at risk” with increasing frequency from the mid-1980s. This paper critically examines research in Galapagos and calls for an increased focus on social sciences in an integrated and holistic research framework. In particular, I emphasize the need for the Galapagos archipelago to be viewed as an integrated “human ecosystem” rather than as a natural ecosystem in which people are adjuncts.

The presentation of solely biological information, without placing this information in a social and cultural context, will deepen conflicts between researchers and the local community and national decision-makers. These conflicts and the absence of social, economic and cultural information will not serve the long-term conservation of the islands. As in the 1950s, there is a need for a paradigm shift in Galapagos research to include more explicitly the social and cultural sciences so as to address the now more complex conservation problems.

This paper presents a possible model for examining socio-ecological interrelations and to help identify gaps in our understanding of the Galapagos human ecosystem.

NOT JUST A “NATURAL” ECOSYSTEM

The Galapagos Islands have been long recognized for their unique characteristics. They are one of the last remaining “pristine” locations, acknowledged as such in 1978 when they became one of the first locations inscribed on the list of World Heritage Sites. Few other tropical archipelagos retain such a high percentage of their native species, a feature that owes much to the late arrival of people (Snell 2002). The islands were discovered in 1535 and subsequently used by pirates, whalers, colonists, prisoners, the military and scientists

(Hickman 1985, Schofield 1989, Whitehead *et al.* 1997, Larson 2001).

From the mid 1600s, the islands became connected to global commerce as privateers used them as a base to attack Spanish sea routes and ports. From the 1700s to the mid-1800s whalers hunted the rich waters to the west and sealers harvested the pelts of the Galapagos fur seal. The islands were annexed by Ecuador in 1832 and saw a series of colonizations linked to agriculture, fishing, penitentiaries and collection of orchil (a lichen), and during the Second World War they were used as a U.S. military base (Hickman 1985, Torre 1996, Larson 2001, Idrovo 2005, Ospina 2006).

The visit of Charles Darwin in 1835 was pivotal for the islands (Corley-Smith 1979, 1987, 1990, Larson 2001). The centennial commemorative visit to the islands in 1935 coincided with the first legal protection of Galapagos in 1934 and 1936. These actions were concreted, after the war, by the formation of the Charles Darwin Foundation in 1959 and official inauguration of the Charles Darwin Research Station in 1964 (Corley-Smith 1990). Tourism began in the late 1960s with the support of the Charles Darwin Foundation and Government of Ecuador (de Groot 1983, Tindle 1983, Kenchington 1989, Epler 1993, 2007, MacFarland 2000). Subsequently, tourism has been the driver of economic and human population growth (Epler 1993, 2007, MacFarland 2000, Grenier 2007a, 2007b, 2007c, Watkins & Cruz 2007). This growth has, in turn, been the basis for an increasingly complex institutional, political and cultural environment that requires constantly shifting organizational and educational strategies.

Today, Galapagos is integrated into worldwide markets for tourism and fisheries and is tied into international consciousness through conservation and the research legacy of Charles Darwin. Galapagos also finds itself under growing pressures in the face of strong international markets and demands from the local community

for greater inclusion in enterprises. The islands are a destination for visitors and transient resource users and five of the islands are home to a population drawn primarily from mainland Ecuador. The archipelago is linked to global social networks and plays a role in global education and research. These connections influence the development options and ecology of the Galapagos and over the past 20 years connectivity to the outside world has grown considerably. Growth appears cyclical with an expanding economy driving an increasing population which in turn increases demand for economic growth; several authors have argued that this rapid globalization is not sustainable (Taylor *et al.* 2006, Grenier 2007a, 2007b, 2007c, Watkins & Cruz 2007).

RESEARCH: A BIOPHYSICAL FOCUS

Research in Galapagos began with the visit of Charles Darwin to the islands in 1835. Darwin focused on geological and biological issues and his visit triggered numerous subsequent research and collecting expeditions including those of Louis Agassiz in 1872, the California Academy of Sciences and Stanford University (Beck 1903, Larson 2001). In the early 1900s, the Smithsonian Institution, the New York Zoological Society and many private naturalist expeditions visited the islands (Beebe 1924, Allan Hancock Foundation 1943, Lack 1945, Larson 2001). Until the Second World War, Galapagos research was almost exclusively biophysical or utilitarian in the case of collecting trips for museums and zoos.

During the 1950s a shift in research focus occurred in Galapagos, reflecting a global trend: researchers became increasingly interested in the conservation and protection of the islands (Eibl-Eibesfeldt 1958, 1960, Bowman 1960). Strong scientific interest in the islands resulted in the establishment of the Charles Darwin Foundation in 1959 and the building of the Charles Darwin Research Station in Puerto Ayora in the early 1960s (Corley-Smith 1990). In the 1960s, research in the islands focused on bathymetry, climate, archaeology, botany, marine biology and Darwin's finches; conservation strategies and the need for planning for colonization were also emphasized (Anon. 1963). The Galapagos International Scientific Project focused on evolution, adaptive radiation, animal behaviour, botany, physiology, vulcanology, petrology, plate tectonics, climate, oceanography and the marine environment; interestingly, economic and energy issues were examined in three of the 40 articles (Bowman 1966).

The Galapagos Science Conference in 1972 emphasized the need for multidisciplinary research on the plants, climate, marine environment and invertebrates, and also called for work on human populations, agriculture, land use, fisheries and the impacts of tourism (Simkin *et al.* 1972). Two compendia publications in the 1980s focused on climate, the marine environment, oceanography, geology, plants, invertebrates, reptiles, birds, lichens, tortoises, iguanas, introduced species and conservation

(Anon. 1982, Perry 1984). Bowman's (1984) review of Galapagos's contribution to science and understanding focuses on evolution, predator-prey relations, geology, climate, origins of life, deep-sea vents, natural selection, animal reproductive behaviour and early human colonization. The Compendium of Science in Galapagos (Sitwell 2000) has little content on social and economic issues except for papers on tourism and conservation, but again is focused on invasive species, plants, invertebrates, marine ecology, reptiles and ornithology.

Grenier (2007a) summarized the history of research in Galapagos and found that only 3 % of research publications had been related to policy, tourism and institutions. Taylor *et al.* (2006) and Epler (1993, 2007) lament the absence of economic information and tourism monitoring for management. Of the 7531 references collated by Snell *et al.* (1996) up to 1995, 1.7 % referred to tourism, 2.7 % to education, 0.7 % to economics, 3 % to political and social issues and 0.3 % to agriculture, reflecting the paucity of research on these issues. Over the years of research in Galapagos, there has been interest in understanding the social and cultural aspects of the islands, reflected by several forays into the social sciences (Loza 1981, Rojas 1992, Rodríguez Rojas 1993, Grenier & De Miras 1994, Ospina 2006, Grenier 2007a). These studies were often in support of planning by the National Institute for Galapagos (INGALA). However, there has not been a consistent attempt to build a social science programme in Galapagos.

Historical research in Galapagos has therefore focused on the biophysical sciences (Larson 2001) but this does not provide sufficient information for effective management (Pimbert & Pretty 1997, Johns 2007). The wealth of biophysical research is a testament to an extraordinary history of scientific interest in the islands; but this interest unfortunately makes the paucity of social science all the more obvious.

TIME FOR A CHANGE IN FOCUS

The Galapagos Islands are a social-biological system; changes in the biological are affected by changes in the social and *vice versa*. The natural, social and cultural resources and their dynamics are linked to and governed by social systems, social order and extrinsic and intrinsic cycles. The management of such a system requires a holistic and integrated approach; reductionist and sector- or discipline-based research may miss critical nuances of the system, with unpredictable consequences for management interventions.

The Galapagos ecosystem can be viewed as consisting of various resources that flow within the system and into and out of it (Machlis *et al.* 1999). Social systems, social order, and social cycles within Galapagos determine these flows (Fig. 1). The result is a complex socio-ecological system wherein management actions have consequences that are difficult to predict. Understanding this complexity is important for effective planning. Natural capital in the

islands consists of the biodiversity, energy, nutrients, water, minerals, land and tourism visitor sites. Socio-economic capital includes the available knowledge about the islands, the local population and its capacities, living spaces, transport, tourism infrastructure, productive capacity and available investment capital. Cultural capital includes local beliefs, myths, ideas, values, trust, local identity, local institutions and organizations, and local perceptions.

The Galapagos of the future will be determined by the flows of key resources within the islands and between the islands and the world. Critical resources change over time. The most important flows for the islands at present are of people (tourists and residents), non-native species, fossil fuels, investment capital, goods and products, nutrients and information. The movements of critical

resources are in turn governed by social systems, predictable cycles and social order within the islands. The most important of the social systems are commerce (in particular tourism), justice, health, education, recreation, non-government institutions, donors, government, planning systems, solid waste and water management systems, local sustenance, transport systems and family structures. The most important cycles are political (election) cycles, the El Niño Southern Oscillation (ENSO), vacation cycles and fishing and tourism cycles. Perhaps the greatest determinant in the past of resource flows has been social order: residence and origins of people, informal and formal norms, and the influence of private investors in decision making.

Critically, it is clear that examining only biodiversity, geology and climate in a complex social and ecological

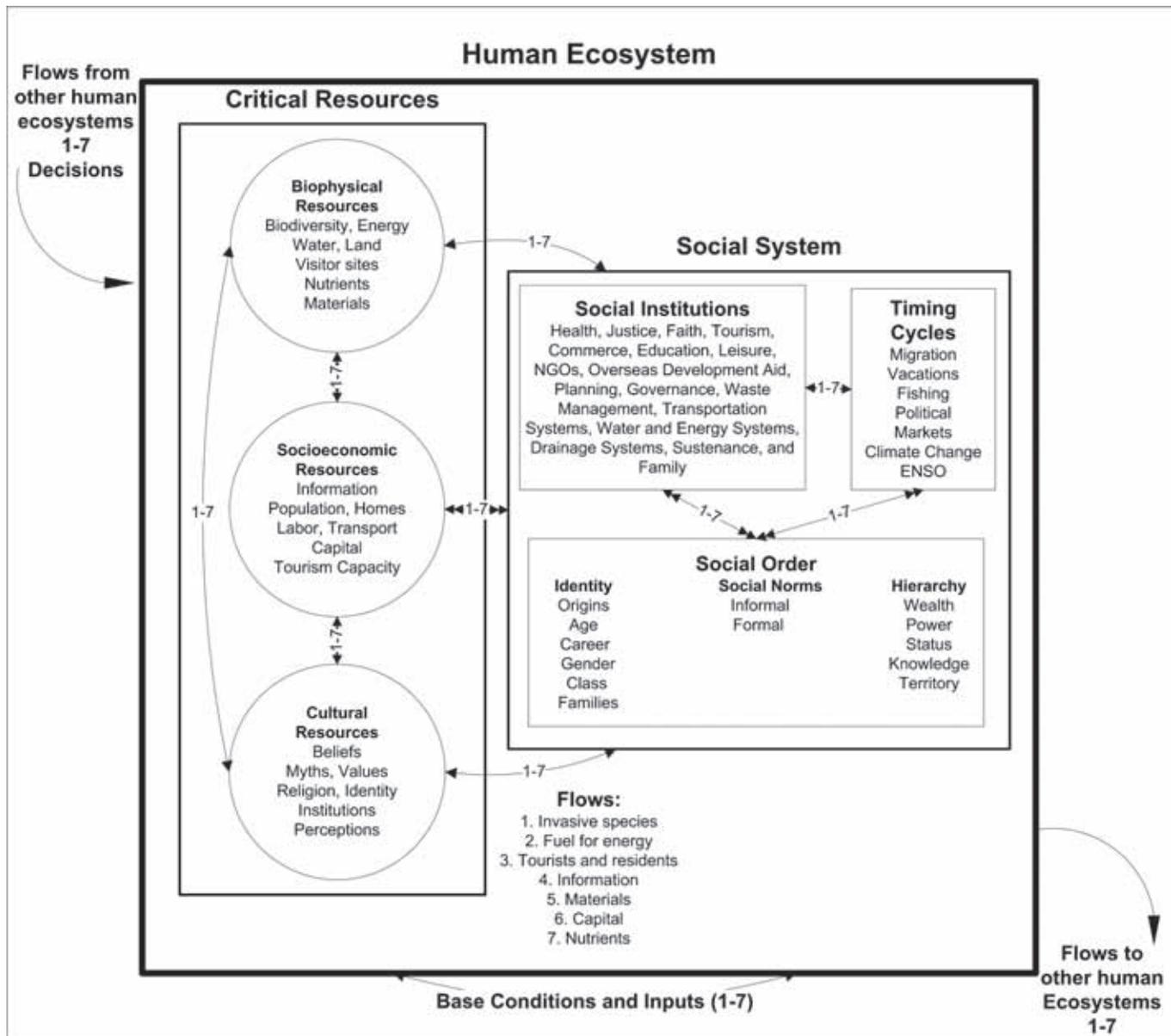


Figure 1. Model of the structure of the Galapagos human ecosystem, adapted from Machlis *et al.* (2005: V.05.2).

system such as Galapagos does not shed sufficient light on the major drivers of change. Socio-economic and cultural resources, water, energy, land use and nutrient flows are critical and not studied enough. Perhaps more importantly, there is little understanding of social systems, social order and social cycles beyond those driven by climatic cycles such as the ENSO. Similarly, a much better understanding of flows of fuel, materials and capital is required for effective management of this system.

THE "HUMAN ECOSYSTEM" APPROACH

Viewing Galapagos using the "human ecosystem" model allows us to evaluate important interactions and guide research priorities. The lack of baseline social and cultural information about Galapagos has been noted (Ospina 2006) and there are few integrated analyses of the problems in the islands (Watkins & Cruz 2007). The problems in Galapagos are frequently multidisciplinary, cutting across the social, cultural and biophysical, as can be illustrated by the following examples. The human ecosystem framework helps analyse the varied and multiple interactions in a complex system by boiling them down to key flows and interactions.

Fisheries management

There is substantial information available on the population biology of sea cucumbers (*e.g.* Toral-Granda & Martinez 2004, 2007, Hearn *et al.* 2005). However, consistently, decisions relating to the sea cucumber fisheries have been taken without adequate understanding of relevant social, economic, political and cultural factors. There has been little research into the political and socio-economic aspects of the fishery, especially on the market forces and capital flows that drive it. It is arguable that the lack of this information and failure to set the fishery in its political, economic, social and cultural context weakened decision making, which has resulted in favouring short term gain and resource depletion over long term benefits.

In the future we will see increased demands for marine resources. Whales, fur seals, tuna, sharks and sea cucumbers were harvested from the waters surrounding the islands; shark fins, sea cucumbers and lobster continue to be exported legally and illegally to markets in the U.S.A. and the Far East. The challenges to managing marine resources will increase as demand increases and it is likely that new marine products will appear for sale from Galapagos. Pressure to permit semi-industrialized access to the pelagic fisheries within the Galapagos Marine Reserve will also increase. The fisheries resources of the islands are also nested in the context of international fisheries issues: the local social ecology of fisheries is embedded in the global, through migrant species harvested outside the marine reserve and through shared markets. The viability of Galapagos fisheries is also highly dependent on climatic and oceanographic cycles and

change. Ultimately, research for effective fisheries management will require an integrated understanding of all of these biophysical, economic, social and cultural aspects.

Tourism

During 2007, the islands were declared "at risk" by the President of Ecuador and by UNESCO's World Heritage Committee. The main concern was the rapid growth of tourism and its influence on immigration, invasive species and pollution. Analyses cited complex and confused governance, conflict among stakeholders, and the failure to implement changes envisaged in the Special Law for Galapagos as the driving forces placing the islands at risk (Boersma *et al.* 2005, UNESCO-IUCN 2007, Watkins & Cruz 2007). Expanding tourism driven by growing global markets is the greatest threat to the Galapagos (Watkins & Cruz 2007) and the response has been inadequate, despite several warnings (Epler 1993, MacFarland 2000, amongst others). Tourism grew exponentially from the 1980s (Epler 2007, Watkins & Cruz 2007, Taylor *et al.* 2006) and drove the rapid growth of settlements in the islands. In the 2006 Galapagos census, 19,140 people were recorded, and over 25,000 are registered by INGALA as permanent residents in the islands. This economic and population growth has in turn driven additional investment in an ever accelerating cycle of growth as small enterprises have grown around tourism and drawn more immigrants to the islands (Watkins & Cruz 2007).

Tourism management in Galapagos proceeded without research and holistic planning to manage such indirect impacts. The tourism model initiated in the 1960s focused on developing national and international private interests because of their international market access and the importance of generating finance for conservation. The model focused on minimizing the direct impacts of tourism on visitor sites through guides and controlled access, but there was little consideration of the role of local residents in tourism or *vice versa* (*cf.* Grimwood & Snow 1966, Schaunenberg 1970, Anon. 1974, 2005, Kenchington 1989, Epler 1993). Today, this tourism model finds itself under severe pressure in the face of demands from the local community for greater inclusion; the apparent alliance between tourism and conservation, reflected in the linking of tourism development with conservation financing has also been questioned (Grenier 2007a).

It is likely that global influences in the Galapagos will continue to grow: tourism is the most rapidly growing business in the world (Taylor 2001, Taylor *et al.* 2006, Epler 2007). As the world has "globalized" so the tourism influence has grown; investment will create more infrastructure, increasing pollution and habitat loss. Small islands throughout the world have seen the need to manage these impacts (Apostolopoulos & Gayle 2002, Douglas 2006); managers will need to address tourism and how it is linked to invasive species, pollution and habitat loss through urbanization, commerce, investment, employment and transport (Watkins & Cruz 2007).

Invasive species

Invasive species present the greatest risk for native and endemic species on isolated islands and archipelagos (Causton *et al.* 2006, Tye 2006). Many domesticated plants and animals were brought to Galapagos since the 18th century, to provide feral food sources and support agricultural development. Threats from these were the focus of early conservation actions, in eradicating goats for example. The globalization of Galapagos threatens to bring more invasive species through international cruise ships, private yachts and direct flights to the islands from other countries. Of perhaps greatest concern are the increasing risks of arrival of diseases and less obvious species such as insects (Kilpatrick *et al.* 2006). Early colonists converted tracts of native vegetation to agricultural use, creating large areas that are now increasingly susceptible to invasive species. The failure to manage the arrival of new invasive species is linked to the failure to establish effective institutional and organizational arrangements for quarantine and to modify the education system in Galapagos to fit local realities; these problems are at root organizational, political and cultural, rather than biological.

Energy use and waste management

Energy requirements have grown with tourism and the human population. Since most energy is still produced from fossil fuels, growth will lead to increased risk of pollution including oil spills. The Jessica oil spill of 2001 (Edgar *et al.* 2003a, 2003b, Gelin *et al.* 2003, Kingston *et al.* 2003) was a warning. Problems of urban pollution, solid waste management and contamination of groundwater in the highly porous volcanic substrate are growing with urban development and a growing population. The increasing numbers of hotels, ships and associated businesses operating in the islands will increase the likelihood of groundwater and marine contamination.

Habitat loss

Various habitats have already undergone substantial anthropogenic change in the Galapagos. Perhaps the most obvious has been the conversion of the highland areas of San Cristobal, Santa Cruz, southern Isabela and Floreana to agricultural zones, stripped of native vegetation and converted into fields that are highly susceptible to invasive species. In addition, there is growing evidence of habitat shifts that result from El Niño events exacerbated by interactions with over-harvesting and over-stocking with livestock, producing circumstances increasingly favourable for invasive species.

THE FUTURE OF RESEARCH IN GALAPAGOS

The gaps in research effort in Galapagos weaken decision making. Integrated research is required to understand complex systems including interactions and flows and communicate results effectively with collaborating

partners. Integrated research would provide critical information on political, social, economic and cultural aspects of Galapagos which, coupled with biological knowledge, will be vital for decision making and understanding of the long term consequences of today's actions. In the absence of integrated information and a shared view of the future of the Galapagos Islands, it is likely that conflicts based on divergent perceptions will increase. It is furthermore likely that the bridges between the local community and research will remain weak, deepening conflicts and impeding management of the consequences of globalization in Galapagos.

The recent "Galapagos at risk" declarations arise from analysis of the remarkably rapid economic and population growth in the islands and the clear links between this growth and increasing risks for biodiversity. The recognition of these risks demonstrates acceptance of the challenges that Galapagos faces, of weak governance, market pressures and globalization of islands that must maintain a degree of isolation in order to maintain their biological and cultural values. The declarations should be viewed as opportunities to implement changes in the islands. Researchers in Galapagos are not without a role in this human ecosystem: they are critical and important players and have the responsibility not only to practice what they preach but also to provide integrated and complete information to decision makers.

One of the major challenges in Galapagos is the absence of a shared view of the present, past or future of the islands. A major challenge has been the failure to incorporate social, economic and cultural understanding with a biological perspective to create a holistic view of the islands: a gap in terms of inventorying the base conditions of this complex human ecosystem. Differences in perceptions and perspectives have been the basis of many local conflicts; the resolution of these conflicts and the capacity to work together will depend to a great extent on developing a shared understanding of the Galapagos socio-ecological system. The justifications for applying integrated research and management approaches to islands were described as far back as the 1990s (Beller *et al.* 1990) and the call for more integrated research in Galapagos has been emphasized in the Galapagos National Park Management Plan (Anon. 2005) and in a recent analysis of social research in Galapagos (Ospina & Falconi 2007).

Developing an understanding of the social ecology of Galapagos will require a shift in research focus. Substantial baseline information remains to be gathered. The integration of social and biological sciences can also serve to draw together distinct players and their concerns. The implementation of a research strategy in the social sciences is a priority to ensure the effective provision of information to the Government of Ecuador to support decision making that will ensure the future conservation of the islands.

The human ecosystem model presented here is one of many that can be used to frame appropriate research questions. Irrespective of the model we employ, we need

to accept that we are working in a socio-ecological system and that understanding this system requires collaborative integrated research. Ospina & Falconi (2007) indicate major gaps in our understanding of agriculture, real estate, land use, quality of life, reproductive health, lives of children, drug use, security, youth, violence, communication and international cooperation. They indicate the need to prioritize research on economic growth, limits, governance, planning processes, culture, identity and tourism. Priority social, economic and cultural research should include, but not be limited to, the following key areas partially derived from Ospina & Falconi (2007):

- Geography: understanding local and national politics, economics, and the culture and social ecology of the Galapagos including analyses of limits to growth and economic constraints and the breakdown of the geographical isolation of Galapagos.
- Economics: understanding financial and economic flows, equity, investment and credit, market cycles and the social and economic consequences of tourism development.
- Assets: understanding human resource management, the regulation of immigration, and employment including capacity building, health systems, education systems and human resources.
- Politics: understanding governance, decision making, institutions, organizations and politics of the Galapagos including public sector administration and conflict resolution.

Ultimately, the establishment of a model for understanding and integrating social and biological sciences in Galapagos is an important step towards providing the necessary information for decision making for a sustainable future in the islands. Integrated human ecosystem approaches are increasingly being applied in the world and are exemplified in calls for interdisciplinary analysis in conservation (Johns 2007), the Millennium Ecosystem Assessments and the National Science Foundation's new Coupled Natural/Human Systems grants.

The Galapagos has suffered years of "crisis" management with incomplete information on the social and cultural systems in the islands. In 2007, the crisis was recognized nationally and internationally. We need to begin to view the islands as a holistic system, with research efforts to encompass and integrate the biophysical, social, economic and cultural sciences, without forgetting the extremely rich and critically important history of biophysical research in the islands.

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THE CHALLENGES IN GALAPAGOS: A VIEW FROM UNESCO

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SUMMARY

We summarise the history of the recognition of the values of and threats to Galapagos, the challenges in charting a path to sustainable development of the islands, and the role of the United Nations Educational, Scientific and Cultural Organisation (UNESCO) in these processes.

RESUMEN

Los retos en Galápagos: una visión desde la UNESCO. Una revisión breve a la historia del reconocimiento de los valores y amenazas de Galápagos, nos permite trazar un camino para el desarrollo sostenible de las islas y plantear el rol de la Organización de las Naciones Unidas para la Educación, la Ciencia y la Cultura (UNESCO) en estos procesos.

BACKGROUND

Galapagos is famous as a natural laboratory for studying evolutionary processes, for its biodiversity and as an example of the transformations that occur in a complex socio-cultural island setting, and the islands have received many recognitions and distinctions. Galapagos is a National Park, a Marine Reserve and perhaps the best conserved tropical oceanic archipelago on the planet. At the request of the government of Ecuador, in 1978 the United Nations Educational, Scientific and Cultural Organisation (UNESCO) declared the Galapagos Islands the first Natural World Heritage (WH) site. In 1984, the islands were declared a Biosphere Reserve. In December 2001 the World Heritage Committee included the Marine Reserve in the WH site.

However, this worldwide recognition has fostered rampant growth of tourism, which has caused exploding immigration and urbanism and the well-known socio-environmental impacts discussed elsewhere in this volume. In April 2007, responding to a request from the national authorities, UNESCO and IUCN conducted a joint mission to evaluate the state of conservation of the WH site and verified that it was seriously endangered by several factors, including the uncontrolled increase of tourism (annual rate of tourism growth between 1990 and 2005 of 14 %: CDF *et al.* 2008), increasing invasions by introduced animal and plant species (Tye *et al.* 2008), and increases in the human population and pollution. During the mission, the UNESCO-IUCN team held several meetings and workshops in Galapagos and Quito with key stakeholders.

The results of this mission were presented in the 31st session of the WH Committee in Christchurch, New Zealand, July 2007, where the Committee adopted Decision WHC-07/31 COM 7B.35 inscribing the Galapagos Islands in the list of World Heritage in Danger. This decision was sustained by Executive Decree No. 270 issued by the

president of Ecuador, Rafael Correa, which declared the Galapagos Islands at risk and its conservation and environmental management a national priority. The decision of the WH Committee included a request to Ecuador to present a first report by 1 Nov 2007, on the measures implemented by the government after the inclusion of Galapagos in the list of WH in Danger. The government's report was submitted, with information on the advances made based on the new policies adopted.

THE ROLE OF UNESCO

The inclusion of Galapagos in the WH in Danger list alerts the national and international community to the serious threats the islands face and calls them to join efforts to respond to the conservation needs of this WH site. In this context, at the request of the Ecuadorian government, UNESCO has ratified its commitment to the conservation and the sustainable development of the natural heritage of Galapagos and its willingness to continue providing technical assistance for Galapagos to achieve the management conditions required for its removal from the WH in Danger list, in the shortest time possible.

UNESCO has set in motion several technical assistance and institutional support processes to assist in saving the site, among them technical support for the design and implementation of Integral Educational Reform in Galapagos, which will incorporate a vision of development and conservation of natural resources. UNESCO will sign a Cooperation Agreement with the Ministry of Education establishing the institutional responsibilities to fulfill this objective. Meetings and workshops have been held in Galapagos to take this forward.

UNESCO has also, in November 2007, granted a *Vocations Patrimoine* scholarship to an Ecuadorian student to undertake doctoral studies on conservation. The student will carry out a comparative study of the management procedures of the protected zones of Galapagos and

the California Channel Islands (U.S.A.), and hopefully contribute to developing improved management. The candidate was selected through the Ecuadorian National Commission for Cooperation with UNESCO.

THE NEXT 50 YEARS

The complexity of the social, political and environmental problems in Galapagos makes it difficult to formulate an outlook for the next 50 years, especially in the current global and national political context; however, we outline some of the main challenges for a common vision of the management and sustainable development of the islands.

Galapagos has attracted much international technical and economic assistance, and many studies have alerted the population, the government and the international community to the serious social, political, economical and environmental threats. However, the national authorities have not always used this information to guide the development, growth and conservation of the islands, while international assistance agencies have not always taken into consideration the conservation and development priorities of the islands, but have based their efforts more on their own priorities, which has limited their positive impacts.

The government of Ecuador, with international support, has started some processes to attend to the problems in the islands (among others: MAE Galapagos Initiative 2020; GEF-UNDP Invasive Species project; IADB Environmental Management Program; AECI Araucaria XXI Program; GMR Management — JICA and USAID; IADB-MIF Production Alternatives; Pro INGALA Italian Cooperation). But at the same time, some political and economic actions are increasing the pressures and threats to the archipelago.

It is thus essential that the national and international community reach a single approach for understanding the problems, and defining long-term tendencies and potential intervention strategies responding to an integral vision. It is also important to include external factors such as the effects of climatic change that could affect the islands in the near future. Plans for long-term sustainable management should have a scientific basis but should also take account of the development options demanded by the local population. Most observers agree that the challenge is to reach a consensus amongst the State institutions, civil society and international cooperation, on clear, concrete and effective policies for maintaining and conserving Galapagos. How to arrive at such a consensus? We present an outline for discussion which attempts to trace a critical route to manage effectively the processes of dialogue, negotiation and governance, through democratic processes.

A prime factor will be the government's willingness to ensure open debate when determining social, economic, environmental and development policies, to ensure the participation of civil society, central and local governments and non-governmental agencies in Galapagos, as well as

to establish their institutional responsibilities and roles in implementing an agreed strategy. The current political context of the National Constitutional Assembly presents an unparalleled opportunity to establish overarching principles for the future of Galapagos as world heritage. The current Ecuadorian administration has taken decisive action by recognizing that Galapagos is at risk and that its conservation is a national priority.

A second aspect is the need for specific action on priority issues, including education, health, quality of life of the local population, natural habitats, biodiversity conservation *etc.* In this respect, it is important from the standpoint of the objectives of the Biosphere Reserves and World Heritage programmes to pass on the lessons learned to a global audience.

A third concern is the urgent need to find a common language for communication between researchers, students, teachers, politicians, decision-makers, cooperation agencies and government authorities, to enable constructive exchange of ideas on the full range of key issues. It is necessary to communicate publicly and fully the findings of the natural and social sciences without sacrificing scientific rigour, so that the knowledge generated by research done in Galapagos can be used by civil society. The time is ripe to develop the communication and popularization of science and technology as instruments for the formulation of policies and for taking technical and opportune decisions.

A fourth requirement is the need for Integral Education Reform in Galapagos, so as to offer quality education that meets the special needs of the local environment and population. This process must include a thorough review of the islands' educational sector in order to define the policies, vision, strategies, content and structure, the educational processes and the administrative mechanisms for implementing the reform.

The final point concerns international cooperation. To make international support more effective, agencies should focus their assistance on responding to plans and proposals of the national government that aim to achieve sustainable development in the islands (*e.g.* the GNP management plan, executive decrees *etc.*) based on a common understanding of the islands' particular circumstances and outlook. It is essential that the national government and the cooperation agencies jointly analyze the socio-economic, political and cultural dynamics of a society that is growing daily and thus places greater demands on its natural resources (drinking water, energy, land and biodiversity). This requires investment in human capital to ensure the islands' survival, as they become increasingly vulnerable to pollution, waste and misuse of natural resources.

CONCLUSION

UNESCO recognizes the renewed efforts of the government of Ecuador and local authorities towards creating

circumstances favourable to the sustainable management of Galapagos, and is encouraged by the positive attitude on the part of international cooperation organizations. The openness shown provides a grand opportunity to discuss, determine and implement the fundamental changes required to ensure long-term sustainable development of the islands. The WHCom-mittee decision to declare Galapagos as heritage in danger should be understood as Ecuador's opportunity to call on the national and international community to take up new challenges, based on

a shared understanding of the problems, opportunities and possibilities for the future of the islands.

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THE RESTORATION OF GIANT TORTOISE AND LAND IGUANA POPULATIONS IN GALAPAGOS

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SUMMARY

The giant tortoise *Geochelone* spp. and land iguana *Conolophus subcristatus* programs of the Charles Darwin Foundation and the Galapagos National Park Service are two of the longest running and most successful conservation programs in the archipelago. Both involve a combination of captive breeding and rearing, repatriations, protection of nests in the field and introduced animal control. They have resulted in larger and healthier populations on several of the islands. This success was accomplished through the integration of scientific research and natural resource management.

RESUMEN

La restauración de las poblaciones de tortugas gigantes e iguanas terrestres en Galápagos. El programa para las tortugas gigantes *Geochelone* spp. e iguanas terrestres *Conolophus subcristatus* de la Fundación Charles Darwin y el Parque Nacional Galápagos son dos de los más largos y exitosos programas de conservación en el archipiélago. Ambos involucran una combinación de reproducción y crianza en cautiverio, repatriación, protección de nidos en el campo y control de animales introducidos. Poblaciones más grandes y sanas en varias de las islas han sido el resultado. Este éxito fue logrado por medio de la integración de la investigación científica con el manejo de los recursos naturales.

INTRODUCTION

The rearing and repatriation of giant tortoises *Geochelone* spp. began at the Charles Darwin Research Station (CDRS) in 1965 and is one of the longest running and most successful programs of the Charles Darwin Foundation (CDF) and the Galapagos National Park Service (GNPS). This program, as well as the land iguana *Conolophus subcristatus* program that began in the 1970s, exemplify many of the most important aspects of the missions and strategic lines of action of these two institutions, including:

- conservation and restoration of species and habitat;
- integration of research and management;
- collaboration with other institutions, including with each other;

- involvement of visiting scientists and consultants;
- education and training, via the volunteer and scholarship program;
- community involvement, such as with the tortoise programs in Isabela;
- tourism, with rearing facilities and corrals of adult tortoises attracting many visitors;
- international workshops and resulting plans of action, such as the 1988 Herpetology Workshop;
- threatened species work catalysing invasive species management programs.

A primary threat to the terrestrial fauna of Galapagos is introduced species, including competitors, predators, and disease, which impact the populations directly and also indirectly through habitat destruction. Growth in

tourism and the related rampant growth in the resident human population combine to increase the threat to native and endemic species not only through the increased risk of new introductions, but also through associated problems, such as development, consumption and waste generation.

Of all of the Galapagos species that were over-exploited historically, giant tortoises were the most affected. Once exploitation by humans decreased, they were then under attack by a myriad of introduced species. Land iguanas, on the other hand, were never a major target for exploitation. However, once feral cats *Felis catus* and dogs *Canis familiaris* entered their domain, their survival was at risk.

THE GIANT TORTOISE PROGRAM

Giant tortoises were among the most devastated of all species in the Galapagos Islands. Only the endemic rice rats (Tribe Oryzomyini) were hit harder, with the majority of species now extinct. Humans first exploited giant tortoises as food; a practice that continues today at a much lower rate. In later years, they were harvested for oil. Some introduced species (primarily rats *Rattus*, pigs *Sus scrofa*, dogs and the *Solenopsis* fire ant) prey on tortoises (particularly eggs and young), while others (goats *Capra hircus* and donkeys *Equus asinus*) damage or destroy tortoise habitat.

With the establishment of the Galapagos National Park and the CDF in 1959, a review of the status of the tortoise populations began. Only 11 of the 14 original populations remained and most of these were endangered if not already on the brink of extinction. The breeding and rearing program for giant tortoises began in response to the condition of the population on Pinzón, where fewer than 200 old adults were found. All of the hatchlings had apparently been killed by introduced black rats *Rattus rattus*, for perhaps more than a century. Without help, this population would eventually disappear. The only thing saving it was the longevity of the tortoise. The rearing program began with the first transfer of eggs from Pinzón to the new tortoise center on Santa Cruz in 1965. In 1970, the first 20 tortoises were repatriated to Pinzón after they had reached an age and a size at which they were considered "rat-proof."

Within a few years, several other tortoise populations were included in the program. Other than the Pinta population, where only one tortoise remained (Lonesome George), the Española population, with only two males and 12 females, was the only population on the brink of extinction. The 14 tortoises eventually found on Española were brought into captivity between 1963 and 1974, and the rearing center also became a breeding center. Eggs and hatchlings were brought from natural nests in the wild from Santiago, Santa Cruz, Isabela (Cerro Azul, Sierra Negra, and Wolf volcanoes), and San Cristóbal. Problems in these populations included low population numbers,

nest destruction by pigs, dogs and *Solenopsis*, habitat destruction by goats and poaching by fishermen and residents.

The tortoise program is one of the best examples of the integration of research and management to achieve conservation goals, attained through cooperation between the CDF and the GNPS. In the 1960s, the research was aimed at determining the status of the populations. Fieldwork identified the threatened populations and the level at which they would be included in the program (breeding population in captivity, tortoise eggs and young brought into captivity, or nest protection or pig control in the field). In the 1970s, the field research began to include behavioral study, to determine the requirements for successful breeding, nesting, and rearing. These results were then incorporated into the management practices at the tortoise center. In the 1980s, experiments in the center focused on determining the best incubation and rearing procedures, with the results also immediately incorporated into the program.

In 1988, the CDF and GNPS hosted an international workshop "The Herpetology of the Galapagos Islands", to review the history of herpetological research and management in Galapagos and develop recommendations for the future. Over 70 scientists, administrators, naturalists and resource managers participated. A series of specific conclusions and recommendations resulted, many of them directly applicable to the breeding and rearing programs. They provided a framework for planning, prioritizing, and implementing research and management for the next decade and beyond.

By 1990, the center on Santa Cruz included tortoises from Española, Pinzón, Santiago, and occasionally Santa Cruz. Wolf Volcano tortoises were removed from the program when more extensive fieldwork demonstrated that the population was much larger than originally believed. Transferring eggs and hatchlings from southern Isabela populations was put on hold in the early 1990s while a second breeding and rearing center was built in Puerto Villamil, Isabela. This center was originally planned during the wildfire of 1985 but was not fully operational until the wildfire of 1994, which coincided with an increase in poaching of tortoises in Isabela. GNPS and CDF personnel took advantage of the focus on the fire to inform the world of the threat from poaching. In addition, helicopters used in fire-fighting were also employed to evacuate tortoises from nearby areas on Sierra Negra where they were threatened due to illegal hunting (but not fire). The Isabela tortoise center houses both breeding adults and young tortoises from southern Isabela.

San Cristóbal tortoises were eliminated from the program on Santa Cruz in the early 1980s when the local human population on that island successfully eradicated feral dogs, the primary cause for the population decline. In 2003, a breeding and rearing center was established at Cerro Verde on San Cristóbal to house some tortoises and to help increase the population.

With improvements in methods resulting from the experiments in the 1980s, the tortoise program had even greater success in the 1990s. Routinely, 500–700 young tortoises (hatchlings to three-year-olds) were reared annually in the center; prior to 1991, the average had been 332 (range 53–462). Average mortality of young tortoises in the center was reduced to <3 % per year, whereas in the 1980s it had been 18 % (range 4.2–31.8 %). The almost factory-like production of young tortoises allowed for the expansion of the program. Areas that received more attention during the 1990s included nutrition and general health, genetic analyses, and expansion of the program in southern Isabela. Much of the work was accomplished with the help of consultants and visiting scientists.

The situation of Lonesome George, the last known survivor of the Pinta population, became of primary concern during the 1990s. Unlike the other tortoises in the center, George became severely overweight. At the end of the 1980s it became apparent that George had to go on a diet. Since that time, veterinarians and nutritionists have examined him periodically and personnel of the center have implemented their recommendations. George was put on public view in a new corral with two females that were brought from Wolf Volcano (thought at the time to be the population most closely related to Pinta tortoises). Genetic analyses have now determined that Pinta tortoises are most closely related to Española tortoises and the replacement of the Wolf females with Española females should be considered. However, after 15 years with no results, the two Wolf tortoises nested in July–August 2008. From the three nests produced, 16 eggs have been placed in the incubators (14 are considered fertile) and are expected to hatch before the end of the year.

Overall, the tortoise program is a huge success. In 1990, the first nests of the repatriated tortoises on Española were found, and the first live hatchlings in 1991. The old tortoises in the breeding center of Santa Cruz have grand-tortoises! The 1000th tortoise was repatriated to Española in March 2000. By early 2007, more than 4000 tortoises had been repatriated to their island of origin (Table 1).

Evaluations in the 1990s of the populations on Pinzón and Española indicated 68–77 % survival of repatriated

tortoises on Pinzón and at least 55 % on Española. These are high survival rates for a repatriation program, important factors being that the majority of the natural habitat is still intact, and that the tortoises are reared in semi-natural conditions similar to their native islands.

Genetics have also begun to play an important role in the repatriation program. Research on Española has indicated that the program has resulted in high levels of inbreeding resulting in low levels of genetic variation. Also, a hybrid tortoise, from an Española female and a Pinzón male, has been identified on the island. This suggests that a Pinzón male was inadvertently repatriated to Española in the early years of the program. These results demonstrate the value of rigorous research and of incorporating modern techniques.

Key to the ultimate survival of the giant tortoises is the elimination of introduced mammals, both predators and competitors. On Española, goats, the only introduced mammals, were eradicated in 1978. During the first decades of the program, the other populations were under constant threat from introduced mammals. To support the repatriation program, tortoise protection was carried out in the nesting zones of Santa Cruz, Santiago and southern Isabela. Pigs were regularly hunted during the nesting and hatching seasons. Nests were protected from pigs by constructing temporary rock walls around them.

By the early 1990s, the tortoise population on Alcedo Volcano, one of the largest and healthiest populations in the archipelago, was in trouble. A few goats had crossed the Perry Isthmus, a natural barrier between northern and southern Isabela, more than 15 years previously, and by 1990 their population was exploding and prime tortoise habitat was disappearing at an alarming rate. Worry over the future of the tortoise population spurred a “tortoise summit” held in England in April 1995. This was followed by an international workshop in 1997 to plan the eradication of goats from northern Isabela; Project Isabela was the result. Completed in 2006, Project Isabela achieved the eradication of goats from Pinta, Santiago, and northern Isabela, pigs from Santiago, and donkeys from Santiago and northern Isabela. These successful eradications have had a positive impact on the tortoises and their habitat.

In 2007, an international workshop was held to examine the potential eradication of introduced rodents from the archipelago. The resulting plan is aimed primarily at the eradication of rats from Pinzón. With the eventual success of Project Pinzón, yet another tortoise population will be out of danger and will no longer need the protection of the rearing and repatriation program.

THE LAND IGUANA PROGRAM

In 1959, the status of the extant populations of land iguanas was considered good. Then in 1975, two populations on different islands (Cerro Cartago on Isabela and Conway Bay on Santa Cruz) were decimated in less than six months by feral dog packs. Unlike tortoises, adult iguanas are not

Table 1. Number of giant tortoises repatriated by population and decade, 1970 to 2008.

Population	Decade				Total
	1970s	1980s	1990s	2000–2008	
Española	79	208	696	499	1482
Pinzón	182	86	244	40	552
San Cristóbal	42	13	0	0	55
Santa Cruz	0	67	28	269	364
Santiago	115	90	282	129	616
Cerro Azul (Isabela)	103	102	8	371	584
Sierra Negra (Isabela)	0	51	52	253	356
Wolf Volcano (Isabela)	14	23	3	0	40
Total	535	640	1313	1561	4049

predator-proof. Saving them meant removing them from their natural habitat until dogs were eliminated.

A breeding and rearing center was quickly established, but it was not large enough for all the adults. A management technique used only once before in Galapagos, in the 1930s, was implemented. Thirty-eight Santa Cruz iguanas, about half of the original group brought to the center, were released on the small islets of Venecia off the northwest coast of Santa Cruz. This semi-captive population lived under natural conditions, but the islets had no large areas suitable for nesting. Approximately 100 m³ of soil was moved to Venecia from Santa Cruz and an artificial nesting area built. The population thrived. The iguanas on Venecia breed and juveniles are then repatriated to Santa Cruz. The transfer of iguanas from Venecia to Santa Cruz continues today, approximately every three years.

Knowledge gained in the tortoise center was applied to the iguana center. However, iguanas are much more difficult to maintain and breed in captivity, and field research and experiments in the center were critical to the success of the program. Of primary concern were the physical conditions of the cages and incubation techniques, including temperature and water potential of the substrate. Experiments resulted in the application of the most successful techniques.

However, by the 1990s, the captive land iguanas were in poor condition and not breeding. An animal nutritionist was brought in to review their diet. He developed a diet plan for the iguanas based on previous work with green iguanas, using lentils, quinoa, vitamins, minerals, and other ingredients. Within a short time, the iguanas became healthier and mortality rates declined.

Unlike tortoises, the young land iguanas could not be repatriated to their original habitat unless the introduced predator problem was solved. Dogs eat adult as well as young iguanas, while cats eat only young animals. Once feral dogs had been eliminated on both southern Isabela and northwestern Santa Cruz, iguana repatriations were generally successful (Table 2). Today, both of these populations appear to be healthy. However, cat control trips are carried out periodically to ensure successful recruitment into the populations.

The land iguanas of Baltra have a very different history. Historically, the Baltra iguanas were the largest in the archipelago. However, when the Hancock Expedition visited the island in 1932 and 1933, the iguanas appeared malnourished. Introduced goats had devastated the vegetation. In an attempt to help the iguanas, members of the expedition transferred 70 iguanas to North Seymour, the island to the north of Baltra where there were no land iguanas and no goats. Within 20 years, the iguanas on Baltra disappeared due to a combination of habitat destruction resulting from the construction of the U.S. air base in World War II, predation by dogs and cats, and competition by feral goats. The informal experiment of the Hancock Expedition had saved the Baltra land iguana from extinction.

Table 2. Number of land iguanas repatriated by population and decade, 1982 to 2008.

Population	1980s	1990s	2000–2008	Total
Cerro Cartago (Isabela)	324	70	0	394
Cerro Dragón (Santa Cruz) ¹	184	111	101	396
Baltra	0	94	326	420
Total	508	275	427	1210

¹Includes repatriations to Conway Bay, Cerro Dragón, and Cerro Montura, all in northwest Santa Cruz. Some of the repatriated iguanas in this population came from the semi-captive population on Venecia.

In the 1980s, iguanas from North Seymour (where the population seemed to be in decline) were brought to the breeding and rearing center, with the idea of eventually repatriating the young to Baltra. Given that Baltra has two military bases, air force and navy, iguana repatriations required the collaboration not only of the CDF and GNPS, but also the Ecuadorian Armed Forces. The first 35 young iguanas were released in June 1991. In total, 420 iguanas have been repatriated to Baltra and their survival rate appears high. Recent surveys have shown that both populations, Baltra and North Seymour, are healthy and increasing.

In response to the nutritional problems encountered in the center in the 1990s, a technique similar to that used for tortoise populations was implemented for the Baltra/North Seymour population. Nests were located on North Seymour and eggs and/or hatchlings brought to the center near the end of the incubation season, thus eliminating the need to maintain adults in captivity. The young were reared in captivity during their most vulnerable years and then released on Baltra.

Genetic analyses have highlighted some anomalies in the iguana program. DNA from museum specimens has shed light on potential mixed ancestry among the iguanas of North Seymour. Further studies are examining evolutionary relationships between Santa Cruz and Baltra iguanas and the role they may have played in these findings. Continued application of new methods not only helps to explain the biogeography of the islands but also improve the management programs.

By 2008, the iguana breeding and rearing program was discontinued due to the successful repopulation of the three areas. The last repatriation from the iguana center to Cerro Dragón was in 1991, to Cerro Cartago in 1993, and to Baltra in 2008. Monitoring and transfer of iguanas from Venecia to Cerro Dragón continues every three years and cat control at both Cerro Dragón and Cerro Cartago is carried out about three times per year.

TRAINING

Both volunteers and scholarship students, primarily from Ecuador's many universities, have always participated

in the tortoise and land iguana programs. Several theses have been written based on such studies. Many of the students have gone on to work for the CDF, the GNPS, or other conservation and natural resource management organizations throughout Ecuador and the world.

THE FUTURE

With the eradication of introduced mammals, many of the giant tortoise populations are nearing the point when the breeding and rearing center will no longer be required. Monitoring their populations and restoring their habitat will now be part of larger island restoration programs. On Española, restoration of the *Opuntia* cactus forests that were decimated by goats is beginning. On Santiago, regeneration of the vegetation in the absence of goats, pigs, and donkeys will need to be monitored to ensure that the plant communities return to near-pristine condition, allowing the tortoise population to complete its recovery on its own. When rats are finally eliminated from Pinzón, island restoration and a naturally reproducing tortoise population will become a reality. Work on southern Isabela, where introduced mammals still exist and where poaching of tortoises is more common than elsewhere in the islands, will continue. Current genetic analyses may also highlight small remnant populations that will need intensive management in the future.

On Pinta, where the return of the Pinta tortoise is questionable if not impossible, a plan for restoring the

island, including the return of giant tortoises, has been approved. Since genetic studies determined that the Española tortoise is genetically the closest to the Pinta tortoise, hatchlings from the Española breeding and rearing program will be used to initiate the restoration of that island and re-establish a tortoise population there, on an island now free of introduced mammals.

The land iguana populations are doing well. If we are able to eradicate the cats one day, land iguanas will also be out of danger.

There are now land iguanas back on Baltra and tortoises will soon be back on Pinta. After nearly 50 years of integrated research and management aimed at the conservation of the biodiversity of Galapagos, most land iguana populations are in good shape and all of the tortoise populations are in better condition than when the Galapagos National Park was established in 1959.

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A research and management program with more than 40 years of success is only possible with the passion and dedication of many scientists, park wardens, consultants, students and volunteers. I am indebted to all of them, for their work in the field and in the tortoise and iguana centers, for our many discussions, and for their many reports and publications.

BOTANICAL RESEARCH IN THE GALAPAGOS ISLANDS: THE LAST FIFTY YEARS AND THE NEXT FIFTY

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SUMMARY

We review recommendations made since the founding of the Charles Darwin Foundation in 1959, concerning botanical research for the conservation of Galapagos, and present our suggestions for priorities for the immediate future.

RESUMEN

La investigación botánica en las Islas Galápagos: los últimos cincuenta años y los próximos cincuenta. Revisamos las recomendaciones hechas desde el establecimiento de la Fundación Charles Darwin en 1959, acerca de la investigación botánica para la conservación de Galápagos, y presentamos nuestras sugerencias para el futuro inmediato.

INTRODUCTION

Since the establishment of the Charles Darwin Foundation (CDF) in 1959, a tremendous amount of botanical research has been accomplished through the collaborative efforts of the Charles Darwin Research Station (CDRS), the Galapagos National Park (GNP), visiting scientists, and local and international volunteers. The direction of this research has often been influenced by the suggestions of experts who have, from time to time, met to discuss and prioritize botanical studies in the archipelago. In this paper, we briefly discuss the history of botanical planning, the major research areas that have been suggested or initiated as a result, and our recommendations for future directions.

BOTANICAL RESEARCH PLANNING SINCE 1959

A landmark in the history of Galapagos botany was the Galapagos International Scientific Project, in 1964. For several weeks, experts from a variety of fields attempted to gather as much information as possible about the natural history of the islands. Botanists participating in the project included E. Yale Dawson, F. Raymond Fosberg, Syuzo Itow, Charles M. Rick, William A. Weber, and Ira L. Wiggins, who generated many ideas for future studies in the archipelago, and contributed to the production of the islands' flora (Wiggins & Porter 1971).

Eight years later, the Galapagos Science Conference, held at the Smithsonian Institution in Washington DC, 6–8 October 1972, attracted botanists including Rick, Wiggins, Paul A. Colinvaux and Duncan M. Porter, and encompassed research planning discussions that recommended: 1) vegetation mapping and quantitative sampling, 2) studies of plant-animal interrelationships, 3) phytogeography, 4) reproductive ecology, and 5) population biology (Simkin *et al.* 1972).

The next and largest gathering of botanists in the Galapagos Islands was the Workshop on Botanical Research and Management held at CDRS, 11–18 April 1987, whose participating scientists are listed in the proceedings (Lawesson *et al.* 1990). The purpose of this meeting was to compile botanical information of use in managing and conserving the flora of the islands. Major recommendations were summarized as: 1) eradication of introduced animals, 2) eradication of introduced plants, 3) protection of endangered species, 4) development of a documentation system, 5) a mapping program, and 6) conservation of Galapagos species outside the islands.

In May 1999, an international workshop of conservation biologists was held at CDRS and GNP headquarters, to produce a "Biodiversity Vision for the Galapagos Islands", with major input from staff and visiting botanists and resulting in more recommendations for the next 50 years (Bensted-Smith 2002). Most recently, the CDRS Botany Department produced a report on recent research and more specific plans for the future (Tye 2003), including: 1) completion of baseline inventories, 2)

establishment of long-term monitoring programs, 3) design and implementation of invasive plant prioritization systems and completion of the Galapagos plant red list, 4) invasive species research and management, 5) habitat protection and restoration, and 6) research and restoration of endangered species.

Aside from the publications mentioned above, which resulted directly from these workshops, other landmark works stimulated by these planning exercises have included major studies of Galapagos vegetation (Werff 1978, Hamann 1981), studies of non-vascular taxa (Weber & Gradstein 1984), a revised checklist of the flora (Lawesson *et al.* 1987) and a field guide (McMullen 1999). Research stimulated by the recommendations listed above has resulted in hundreds of journal articles and book chapters. The Galapagos bibliography up to 1995 (Snell *et al.* 1996) includes more than 1000 references to botanical keywords.

RECOMMENDATIONS FOR FUTURE DIRECTIONS

Although many of the research topics suggested by previous groups have been at least partially tackled, most have yet to be completed and others remain to be initiated. Taking into account the previous recommendations cited above and placing priority on research applied to conservation, we list here some important areas that need to be addressed or continued in the next 50 years. These are listed, as far as possible, to correspond with the order of the research framework of the CDF Strategic Plan (Charles Darwin Foundation 2006), *i.e.* baseline, monitoring, prioritization, research on priorities, experimental management.

Support services

Maintain a comprehensive herbarium collection, as an important reference tool for botanical research, especially floristic and systematic studies.

Establish an efficient information management and geographical information system for all herbarium collections at CDRS and incorporating data from elsewhere.

Establish an information management platform to make plant specimen and other data from CDRS collections and elsewhere accessible via the internet, including high resolution scans of specimens.

Complete and publish comprehensive checklists for all Galapagos plants, including non-vascular taxa, fungi and lichens.

Produce a revised flora of Galapagos.

Produce illustrated identification materials accessible in both English and Spanish, covering vascular and non-vascular plants, fungi and lichens.

Baseline studies

Complete comprehensive surveys of all islands to improve knowledge of the status and distribution of Galapagos plants, including non-vascular taxa, lichens and fungi, and with emphasis on endemic and threatened species.

Produce new and improved digital vegetation maps of the archipelago.

Monitoring

Implement and expand community and species monitoring for high priority threatened species and habitats, and for invasive species including monitoring for new introductions.

Prioritization

Complete and periodically revise red lists, including non-vascular species, lichens, fungi and marine plants, and produce Galapagos Plant Red Data Books.

Maintain and update the Galapagos Weed Risk Assessment system.

Studies of priority species, communities and problems

Implement studies to determine the threats to and causes of population declines of the highest priority threatened endemic plants (Critically Endangered species and "lost" species with no recent records).

Continue taxonomic revisions of endemic plant groups, to clarify conservation priorities and species distributions.

Investigate the biology, ecology and population dynamics of Galapagos native plants, especially endemic and threatened taxa, including pollination ecology, herbivory, seed dispersal and the impacts of introduced plants and animals.

Investigate the biology and impacts of high risk invasive and potentially invasive species, and design effective control measures.

Conduct studies of vegetation dynamics, including primary and secondary succession, especially in relation to disturbance, invasive species and the outcomes of management practices, to improve the latter.

Management

Establish a seed bank of endemic plants.

Implement restoration projects for the highest priority threatened endemic plants (Critically Endangered) and vegetation communities.

Implement management projects for high risk invasive species, using best practice design for the choice of management goals and techniques, including monitoring to determine effectiveness of control and recuperation of the native habitat and communities.

To realize these goals, a continuation of the CDRS botanical research program, with close collaboration with the GNP and productive research alliances with outside experts, universities and research institutes, is

essential. Equally important is the continued training of young scientists, which has been a strength of CDRS. The interest and voices of future generations of Ecuadorian and other botanists and conservationists are the best insurance that this work will continue for the next 50 years.

ACKNOWLEDGMENTS

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MANAGEMENT OF INTRODUCED ANIMALS IN GALAPAGOS

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SUMMARY

We review programmes to control or eradicate introduced vertebrates and invertebrates in Galapagos.

RESUMEN

El manejo de los animales introducidos en Galápagos. Revisamos los programas de control y erradicación de vertebrados e invertebrados en Galápagos.

INTRODUCTION

The arrival of humans in the Galapagos Islands, since their discovery in 1535, brought a series of negative impacts and, in some cases, irreversible damage, such as the extinction of endemic plants and rodents on several islands. A major cause of these impacts was the deliberate or unintentional introduction of non-native organisms. There have been substantial efforts to eradicate introduced species on the islands over the last 20 years and, in other cases when it has not been possible to eradicate a species, control activities have at least reversed negative impacts.

INTRODUCED VERTEBRATES

As of 2007, 36 introduced vertebrate species had been recorded in Galapagos, of which 30 had become established; the other six were detected and eliminated on arrival (Jiménez-Uzcátegui *et al.* 2008). Some were brought as food for the human population and do not threaten the island ecosystem, while others were brought unintentionally, or as pets or domesticated animals that escaped to form wild populations (Jiménez-Uzcátegui *et al.* 2008). At present, efforts of the Galapagos National Park and Charles Darwin Foundation are focused on control and eradication programmes for feral Goat *Capra hircus*, Pig *Sus scrofa*, Donkey *Equus asinus*, Cat *Felis catus*, Black Rat *Rattus rattus*, Brown Rat *R. norvegicus* and House Mouse *Mus musculus*, and on promoting the recovery of native ecosystems and of endemic species affected by these introduced animals.

Eradication of feral Goat

Many goat eradications have been carried out successfully in Galapagos (Table 1, see Campbell *et al.* 2004, Campbell & Donlan 2005). Since 2004, goat eradication projects on Santiago, Isabela and Floreana islands have used three phases: an aerial hunting phase using a helicopter, especially when there is a large number of goats; a land hunting phase using groups of hunters aided by specially

trained dogs; a monitoring phase using radio tagged "Judas goats" that associate with remaining feral animals, after the goat population has been significantly reduced by aerial and land hunting. Goat eradication projects on Isabela and Santiago islands reached the monitoring stage in 2006. At the end of 2006, a goat (and donkey) eradication program was begun on Floreana, and was thought successful by 2008. Monitoring will continue in order to ensure successful eradication.

Eradication of feral Pig

Pigs were eradicated from Santiago at the end of 2001, after almost 25 years of work. In the early 1990s, activities were intermittent, but an injection of donated funds in 1998 made possible an intensive campaign combining various techniques, including systematic dog-aided hunting and the use of anticoagulant poisons. From the 1970s to the end of the operation, *c.* 18,800 pigs were eliminated on the island (Cruz *et al.* 2005). On Sierra Negra and Cerro Azul volcanoes of Isabela Island and on Santa Cruz Island long-term pig control is being done to reduce predation on tortoise nests.

Eradication of feral Donkey

Donkeys were eradicated from Santiago Island, where park wardens gradually eliminated them over several decades; the last 24 individuals were shot from a helicopter in 2004, during the Isabela Project (Carrión *et al.* 2007). Donkeys were eradicated from Alcedo Volcano, northern Isabela, where *c.* 1523 individuals were exterminated between 2004 and 2005, only 99 of them with helicopter support (Carrión *et al.* 2007). During the Isabela Project, *c.* 1102 were killed on southern Isabela, where it is estimated that about 200 live animals remained at the end of 2007. Floreana's total donkey population of 302 was eradicated at the beginning of 2007.

Eradication of feral Cat

Cats were eradicated from Baltra Island in 2004. This was possible because the island is small (2.6 km²), has a small

Table 1. Galapagos islands from which feral Goat has been eradicated.

Island	Area (ha)	Ngoats eliminated	Year eradicated
Plazas Sur	13	5	1961
Santa Fe	2,413	3,005	1971
Rábida	508	14	1975
Española	6,089	3,344	1978
Marchena	12,996	484	1983 and 2002
Pinta	5,910	40,000	1999
Santiago	57,728	85,000*	2006
Isabela (north)	240,000	135,000*	2006
Baltra	2,537	35	2007
Floreana	17,229	1,320	2008
Total	345,423	208,207	

*Includes animals killed before the Isabela Project started in 1998.

human population, low risk of reintroduction, mainly carries sparse open vegetation which facilitates control and monitoring, and has a road network that facilitated access. Behavioural studies revealed that the cats were active both during the day and at night (Phillips *et al.* 2005). Field personnel looked for tracks in the day and set traps (Tomahawk and Victor) where they were found. Nocturnal searching was also carried out using searchlights, and cats spotted were hunted with rifles. This methodology was successful in gradually reducing the cat population until it was completely eradicated, with *c.* 250 individuals eliminated. Monitoring from late 2003 to the present revealed no traces of live individuals, but monitoring will be continued annually to detect possible reintroductions.

Cat control continues at Punta Pitt on San Cristóbal and at Bahía Cartago and on the main southern beaches of Isabela. In 2006, cat control was begun on the west coast of Isabela to prevent predation on important marine bird colonies there, especially penguin breeding colonies.

Eradication of rats

Black Rat and House Mouse probably arrived to the Galapagos on ships at the end of the 18th century, and the Brown Rat in the 1980s. These species are currently spread over several islands and affect endemic species including iguanas, nesting tortoises and birds (Cruz & Cruz 1987a, 1987b). The long-term Black Rat control program began in 1982 in the nesting zones of Dark-rumped Petrel *Pterodroma phaeopygia* on Floreana and was later extended to Santa Cruz, San Cristóbal and Santiago islands. The petrel population on Floreana was soon on the path to recovery (Cruz & Cruz 1987a, 1987b).

A workshop was held in early 2007 in Galapagos, with the participation of international experts in rat management on oceanic islands. This resulted in the first draft of a long-term rat management plan for the archipelago. The first step was an eradication project on

North Seymour Island. After three applications of Klerat (anticoagulant in wax bait blocks) spread manually over the entire island using equidistant point distribution, monitoring suggests that rats have been eradicated.

Eradication of Rock Dove *Columba livia*

The Rock Dove was introduced to San Cristóbal, Floreana and Isabela Islands around 1972–3 (F. Cruz pers. comm.), and reported on Santa Cruz for the first time in 1983. These birds are carriers of at least 40 diseases that can affect humans, wild fauna and poultry, including *Tricomonas gallinae*, a disease that affects the endemic Galapagos Dove *Zenaida galapagoensis* (Santiago-Alarcón *et al.* 2006) and domestic poultry. While Rock Doves are themselves resistant to many of these diseases, they become points of infection for transmission to other birds.

After joint efforts by various local organizations, the Rock Dove was eradicated from the urban and rural areas of Santa Cruz in 2002, with 429 individuals eliminated in *c.* 18 months. The eradication operation on San Cristóbal began in 2002 at Puerto Baquerizo Moreno and in the agricultural zone and 816 pigeons were eliminated using the same methods as on Santa Cruz. In 2004, an eradication project was launched on Isabela in both urban and agricultural zones, and *c.* 400 individuals were eliminated on this island. Regular monitoring continues, to detect and prevent reintroduction of this species.

INTRODUCED INVERTEBRATES

According to the latest data (Causton & Sevilla 2008), 499 identified insect species and 53 other terrestrial invertebrates have been introduced into the Galapagos Islands. Many more remain to be identified and, despite the introduction of the Galapagos inspection and quarantine system, new species continue to arrive and escape detection at control points. The most aggressive of the identified invertebrate species include two fire ants and one scale insect (discussed below), with an additional 58 identified as actually or potentially damaging (Causton & Sevilla 2008).

Eradication of fire ants

An eradication programme for the Little Red Fire Ant *Wasmannia auropunctata* was begun in a 26-ha area on Marchena Island in 2000. The method involved first surveying the relative abundance and distribution of *Wasmannia* and other ants, using sausage, peanut butter, sweet biscuits and canned tuna fish as baits, along with pitfall traps and Berlese funnels. Then monitoring visits were undertaken, with AMDRO (commercially sold as Siege Pro) insecticide bait (hydramethylnon 0.73 g/kg) dispersed over the infested area at the end of each trip. In the last six monitoring visits, since 2002, no *Wasmannia* were found in and adjacent to the treated area, and native ant communities had stabilized (Causton *et al.* 2005). The methodology was thus proved effective and may be used

on other islands. However, during a recent goat monitoring trip to Marchena, ant traps were set in other places outside the treated area and *Wasmannia* was detected at two sites. We urgently need to delimit these infested areas and immediately proceed to eliminate the insects.

On southern Isabela, campaigns to control *Wasmannia* are currently being carried out in the tortoise nesting sites on Cinco Cerros and at the Sulphur Mine in the Sierra Negra crater.

The Black Fire Ant *Solenopsis geminata* was detected on Champion Islet in early 2007 and monitoring was begun to determine the extent of the infestation. Subsequent applications of Siege Pro bait seem to have been sufficient to eradicate this species, which is however common on some of the larger Galapagos islands.

Control of the Cottony Cushion Scale *Icerya purchasi*

Icerya purchasi has invaded some 80 countries, damaging more than 2000 plant species. It was reported for the first time in Galapagos in 1982, where it attacks at least 62 endemic and native plant species and some crops, especially citrus. Infestations were killing mangroves and many threatened endemic plants. Control of *Icerya* was the first scientific use of a biological control agent in Galapagos, with the first individuals of the Australian ladybird *Rodolia cardinalis* released in January 2002, simultaneously on Santa Cruz, San Cristóbal, southern Isabela and Floreana islands. Later, it was released on northern Isabela and uninhabited islands including Marchena, Pinta, Pinzón, Rábida, Genovesa, Santiago and Fernandina. Monitoring on Santa Cruz showed the ladybird's great ability to disperse, with insects found up to 40 km from release points, such as at Baltra, North Seymour and Eden islets. They were observed feeding on *Icerya* on a variety of plants and have brought it under control sufficiently to allow recovery of many severely damaged plant populations.

MANAGEMENT PRIORITIES AND STRATEGIES

There are two alternatives for managing invasive species that are already established in the Galapagos Islands. The preferred option, eradication, involves removing them completely from the islands where they are found, while the second, control and mitigation, involves reducing the damage they cause to levels that do not alter natural ecosystem processes and biological diversity significantly. Eradication is the preferred option, provided it is feasible, as it is more cost-effective in the long term than continuous control. It is increasingly viable because of developments in technology and expertise.

The choice between eradication and control is based on eradication feasibility assessment, and on scientific knowledge of the targeted and non-target species, of the impact of the methods used and of the impact of the introduced species. A fundamental tool to facilitate such decisions will be a prediction system currently under test, which takes into account factors such as the population dynamics and dispersal ability of the introduced species, its impact on the ecosystem, habitats or species, and the costs and resources required for management.

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Galapagos Research

INSTRUCTIONS FOR AUTHORS

Galapagos Research (formerly *Noticias de Galápagos*) is the research journal of the Charles Darwin Foundation for the Galapagos Islands. It publishes Research Articles, archival value news items (“News from Academy Bay”) and more general or popular articles (“Galapagos Commentary”) covering any topic relevant to science or nature conservation in Galapagos, including natural history, biology, ecology, evolution, systematics, conservation biology, geology, geography, history, human activity, and the management of biological diversity. Material from other geographical areas may also be considered, if it is of immediate relevance to science or conservation in Galapagos.

Contributions are accepted in English. Editorial assistance will be made available to authors whose first language is not English, but this does not include full translation from other languages; it is the author’s responsibility to have the paper translated into English prior to submission. Submission by email (Microsoft Word document as attached file) is preferred, to the Editor at <galapagosresearch@fcdarwin.org.ec>. Consult the Editor for further advice.

Research Articles must be original contributions that deal with subjects of relevance to Galapagos science or conservation (including all the subject areas listed above). Material published elsewhere, in whole or in part, will not normally be accepted. Wherever possible, manuscripts should have been critically scrutinised by at least one specialist in the relevant field, before submission to the journal. Papers from Charles Darwin Research Station staff and volunteers should be submitted to their Head of Department for review and approval prior to submission. Submitted manuscripts will be sent by the Editor to at least one relevant authority (normally two) for critical review.

News from Academy Bay items should not normally exceed 1000 words. News items may include notices of happenings in the islands that affect science or conservation, recent or forthcoming major events or publications about Galapagos (including book reviews), achievements in Galapagos science or conservation etc.

Galapagos Commentary items include opinion or discussion of Galapagos science or conservation issues, and more general or popular articles that have relevance to Galapagos science or conservation.

Format of tabular material, numbers, metric units, references, *etc.* should match recent issues. Note particularly: dates should be in the form 2 Feb 1990 but months standing alone in text may be written in full; times of day are written 6h45, 17h32 and coordinates in the form 0°46’ N, 1°4’ W (no leading zeros); numbers up to ten are written in full, except when followed by abbreviated units (*e.g.* 6 m), numbers from 11 upwards are written in figures except at the beginning of a sentence. All references mentioned in the article, and only such, must be entered in the bibliography.

Locality names should be widely recognised and in current use where possible. Articles citing older names, or localities that are not widely known, should contain a map or gazetteer, including all such localities mentioned. **Scientific names** should follow a recognised authority, which should be cited in papers dealing with taxonomic issues or lengthy species lists. Scientific names of **plants** should follow P.M. Jørgensen & S. León-Yáñez (1999) Catalogue of the Vascular Plants of Ecuador. *Monographs in Systematic Botany from the Missouri Botanical Garden* 75 (see <http://www.tropicos.org/> for database), unless sound reasons for following a different scheme are presented.

Figures should be prepared as for final reproduction, allowing for reduction to fit column or page size. Figures prepared in or scanned into an appropriate graphics format, saved at high resolution and submitted electronically are preferred. Figures should not be included in a Word file. Low-resolution files or poor-quality scans will not be accepted. When designing Figures, pay attention to *Galapagos Research* column size and page-shape. Authors are encouraged to submit **photographs** that illustrate salient points of their articles. Photographs should be high-contrast (for publication in monochrome) and high resolution. Photographs should be supplied in graphics file format (*e.g.* jpg or tif) and should not be pasted into a Word file. Consult the Editor for further advice.

All Research Articles (but not News items or short Commentary notes) should include a **Summary**, not exceeding 5% of the paper’s length. The Summary should briefly refer to the major findings of the paper and not simply outline what was done in the study. Summaries will be published in both English and Spanish and will be translated if necessary by the Editorial Board.

Offprints will not be supplied, but authors will be sent one copy of the issue in which their article appears, and a pdf file of their article, *gratis*.

