

# Marine iguanas die from trace oil pollution

A near-miss ecological disaster still left a sinister aftermath for these giant lizards.

An oil tanker ran aground on the Galapagos island of San Cristóbal on 17 January 2001, spilling roughly three million litres of diesel and bunker oil. The slick started to spread westwards<sup>1</sup> and was dispersed by strong currents, so only a few marine animals were killed immediately as a result. Here we draw on long-term data sets gathered before the spill to show that a population of marine iguanas (*Amblyrhynchus cristatus*) on Santa Fe island suffered a massive 62% mortality in the year after the accident, due to a small amount of residual oil contamination in the sea. Another population on the more remote island of Genovesa was unaffected.

Environmental disasters such as oil fouling kill many organisms each year, but the subtle effects of low-level environmental contamination are rarely investigated<sup>2</sup>. Although generally heralded as an ecological catastrophe narrowly averted<sup>3</sup> at the Galapagos World Heritage site (Fig. 1), some oil still persisted around Santa Fe (Fig. 2a), where originally about 1 litre of

bunker oil came ashore per metre of beach; maximal oil concentrations reached 44 parts per million, which is low by international standards (L. Loughheed, G. Edgar and H.L.S., unpublished results).

The investigation of animal populations affected by environmental contamination generally begins in the aftermath of a spill so that the recovery process can be studied — as, for example, in the intertidal communities in Alaska after the *Exxon Valdez* accident<sup>4</sup>. However, in the years before the Galapagos oil spill, we had accrued long-term data sets on two island populations of marine iguanas<sup>5</sup>. We were therefore able to assess the effects of residual low-level oil contamination after the accident on one of these populations by comparing it with the other, whose habitat was unaffected.

We also compared circulating levels of the 'stress' hormone corticosterone in blood samples taken from marine iguanas on Santa Fe immediately before and shortly after the oil spill<sup>1</sup>. We previously argued that



**Figure 1** The tanker *Jessica* ran aground in the Galapagos archipelago in January 2001. Immediate damage to marine life was largely averted as the split oil was soon dispersed, but marine iguana populations in the vicinity fell by more than half during the following year.

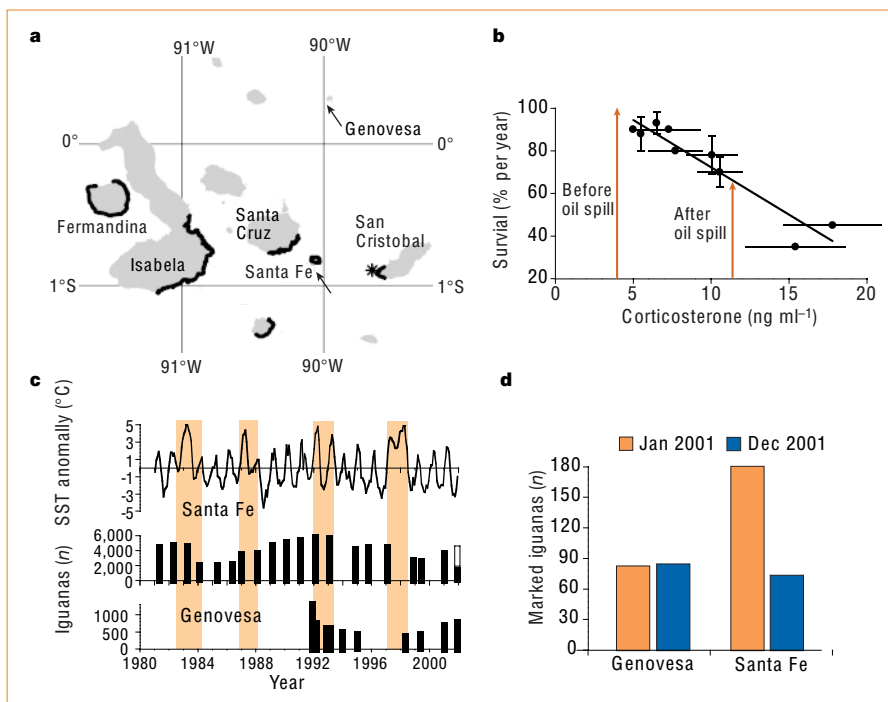
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exposed animals might suffer high mortality (Fig. 2b) as a result of the increased stress they experienced after the spill<sup>6</sup>.

Marine iguanas are herbivorous lizards that are endemic to the Galapagos and feed solely on algae in the intertidal or subtidal zone<sup>7</sup>. Their hindguts harbour specialized fermentation bacteria that break down algal cell walls to facilitate digestion<sup>8</sup>. Adult iguanas are essentially free of predators on both islands, so death is normally caused by senescence or by food shortages, which affect both populations to similar extents<sup>5</sup>. Mark-and-recapture data indicate that there were large population declines during the post-El Niño periods of 1983, 1988, 1992 and 1998 as a result of food shortages (Fig. 2c). These declines were followed by population recoveries during subsequent cold La Niña periods.

Because marine iguanas show strong site fidelity, their mortality can be measured by taking repeated censuses of study colonies<sup>5,6</sup>. We collected this information from the two populations over periods of 20 years (Santa Fe, 90° 02' W, 0° 50' S) and 10 years (Genovesa island, 89° 59' W, 0° 19' N), respectively, before the oil spill, and for 11 months after the oil spill (until December 2001).

Despite the reportedly low degree of oil contamination, several lines of evidence indicate that the pronounced increase in mortality that we observed among the Santa Fe animals was related to the oil spill. First, although food conditions were good, we found an unexpectedly large number of skeletons along the shores of Santa Fe; no skeletons were found on Genovesa. Second, overall iguana numbers in the Santa Fe



**Figure 2** Effect on marine iguanas (*Amblyrhynchus cristatus*) of low-level oil contamination. **a**, Map of the Galapagos archipelago showing the site of the oil spill in January 2001 (asterisk) and the extent of oil contamination (thick lines) along the coastlines of the main islands until 15 February 2001 (data from coastal surveys; L. Loughheed, G. Edgar and H.L.S., unpublished results). Arrows show study sites. **b**, Corticosterone levels induced by 15 min of handling stress can be used to predict the survival of iguanas (redrawn from ref. 6). **c**, Anomalies in sea surface temperature (SST) in the Galapagos since 1980 (top), and population counts in study colonies of iguanas on the islands of Santa Fe and Genovesa. Iguana numbers generally decline during high-SST anomalies (El Niño periods). During 2001, there were more iguanas on Genovesa, as expected from hatching recruitment during periods of low SST (high nutrient abundance), whereas Santa Fe showed a marked decline in numbers (white bar, predicted numbers; black bar, actual numbers in 2002). **d**, The number of permanently marked individuals recaptured during December 2001 was stable relative to January 2001 numbers on Genovesa, but decreased by 62% on Santa Fe.

study colony declined sharply (Fig. 2c). Third, we saw a significant reduction in the number of permanently marked iguanas on Santa Fe (Fig. 2d), whereas those on Genovesa all survived (62% local mortality of marked Santa Fe individuals;  $\chi^2$ -test,  $P < 0.001$ ).

There are four possible explanations for this high mortality in the aftermath of the oil spill. The oil may have had a direct toxic effect either on the iguanas themselves<sup>9</sup> or on the algae they consume<sup>4</sup>; the animals may have declined to eat because their food had been fouled; or their vital hindgut microsymbionts may have been poisoned so that the iguanas could no longer digest their food<sup>10</sup>.

As no deaths occurred immediately after the spill, and algal pastures and foraging were both normal in the 2 weeks after it, we infer that the fermenting endosymbionts in the iguanas' hindgut must be very sensitive to low-level environmental disturbance or contamination. This sensitivity probably compromises the digestive efficiency of affected iguanas<sup>7</sup>, causing their corticosterone concentrations to rise<sup>1</sup> and triggering an increase in mortality.

Our results illustrate the severe effects that low-level environmental contamination can have on wild animal populations<sup>11</sup>. In this context, corticosterone levels are a reliable indicator of the induction of life-threatening stress<sup>6,11</sup>, which correlates with the ensuing mass mortality on Santa Fe<sup>1,6</sup>.

Ecology

Darwin's naturalization hypothesis challenged

Naturalized plants can have a significant ecological and economic impact<sup>1</sup>, yet they comprise only a fraction of the plant species introduced into new areas by humans<sup>2</sup>. Darwin proposed<sup>3</sup> that introduced plant species will be less likely to establish a self-sustaining wild population in places with congeneric native species because the introduced plants have to compete with their close native relatives, or are more likely to be attacked by native herbivores or pathogens<sup>4,5</sup>, a theory known as Darwin's naturalization hypothesis<sup>6</sup>. Here we analyse a complete list of seed-plant species that have been introduced to New Zealand and find that those with congeneric relatives are significantly more, not less, likely to naturalize — perhaps because they share with their native relatives traits that pre-adapt them to their new environment.

We obtained a list of all exotic angiosperm and gymnosperm species that have been introduced for cultivation into

Our findings warn against complacency over apparently low-impact contamination after environmental disasters in other wildlife areas, such as the Arctic National Wildlife Refuge in Alaska.

Martin Wikelski\*, Vanessa Wong\*, Brett Chevalier\*, Niels Rattenborg†, Howard L. Snell‡

\*Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544, USA  
e-mail: wikelski@princeton.edu

†Department of Psychiatry, University of Wisconsin Medical School, Madison, Wisconsin 53719, USA

‡Charles Darwin Research Station, Galapagos, Ecuador, and Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131, USA

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New Zealand, compiled using information obtained from commercial seed and plant catalogues, national agricultural research organizations, herbaria records, botanic gardens, the Ministry of Agriculture and Fisheries, private and commercial arboreta, specialist plant societies, and individuals.

Plant names were validated against the *Index Kewensis*<sup>7</sup>, synonyms were removed, and species were classified by family<sup>8</sup>. The resulting list comprised 24,774 species in 3,863 genera and 262 families. Of these, 1,769 species in 749 genera have become fully naturalized in New Zealand (these are defined as species that form populations that are self-maintained by seed or vegetative reproduction, or that occur repeatedly in wild or urban environments<sup>9</sup>).

Table 1 Classification of seed-plant genera introduced into New Zealand

	Genus contains native species	No		Yes	
		No	Yes	No	Yes
Genus contains	No	2,995	119		
naturalized species	Yes	650	99		
Naturalized genera		18%	45%		

The 3,863 seed-plant genera introduced into New Zealand are cross-classified according to whether or not the genus contains at least one fully naturalized species, and whether it contains at least one native species.

We compiled a list of 1,511 native plant species that occur in genera with at least one introduced species. We separated the 3,863 introduced genera into those that contain at least one naturalized species and those that do not, and into those that contain at least one native species and those that do not (Table 1). Considerably fewer naturalized genera were found to contain native species (650 with no native species; 99 with at least one), but the naturalization rate was much higher among introduced genera that contain native species (45% in genera with native species; 18% in genera without).

To account for likely differences between families in naturalization rates, we fitted a generalized linear mixed model, using PROC NL MIXED in SAS<sup>10</sup>, with the naturalization rate per genus (that is, the number of naturalized species in a genus as a proportion of the total number of introduced species in a genus) as the response variable, a variable coding genera as containing at least one native species or not as a fixed-effect predictor, and a variable coding for family as a random effect.

This analysis revealed that, within families, genera containing at least one native species showed a significantly higher rate of naturalization than genera without native species ( $t_{261} = 6.7$ ,  $P < 0.0001$ ). Furthermore, for the 218 genera with at least one native species, the rate of naturalization was significantly higher in genera containing a greater number of native species ( $t_{83} = 2.9$ ,  $P < 0.005$ , with family included as a random effect and number of native species per genus  $\log_{10}$ -transformed).

Our discovery of a higher naturalization rate in introduced genera containing native species contradicts Darwin's naturalization hypothesis<sup>3–6</sup>. One possible explanation, which was also considered by Darwin<sup>3</sup>, is that introduced species with native congeners are more likely to share features with them that allow survival in New Zealand, compared with introduced species that lack close relatives there. These shared traits may pre-adapt the plants to their new environment, helping to outweigh the potential disadvantage of stronger competition from close relatives<sup>11,12</sup>.

Richard P. Duncan\*, Peter A. Williams†

\*Ecology and Entomology Group, Soil, Plant and Ecological Sciences Division, PO Box 84, Lincoln University, Canterbury, New Zealand  
e-mail: duncanr@lincoln.ac.nz

†Landcare Research, Private Bag 6, Nelson, New Zealand

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