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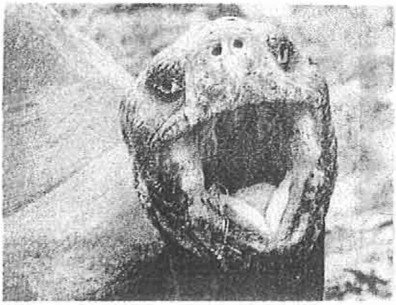


Co-evolution:
Plant form and toothless browsers on the Galápagos Islands.

By Allison Knight

At first it was just going to be a simple family holiday, a cruise around the Galápagos Islands to celebrate Rob's graduation from Princeton. But then the botanists around me at Otago said that they hoped I would report back to the Botanical Society so I realised that perhaps I should pay some attention to the botany. Lichens were the obvious choice, that being my main passion, so I downloaded the list of the 196 lichens, only 11 of them endemic, that have been recorded from the Galápagos, mostly by Bill Weber, who became a helpful correspondent from Boulder, Colorado.

Ecology and Evolutionary Biology at Princeton

But, once we arrived in Princeton, Rob introduced us to various members of the Department of Ecology and Evolutionary Biology. With the "Divarication – defense against toothless browsers?" debate revived by William Bond at our AGM still turning over in my mind, I couldn't resist asking if any of them knew of any examples of plant modification in response to browsing. Henry Horn, who bills himself as Boy Wonder Emeritus and makes art work out of computer innards, told us of a fir tree that has browse-resistant juvenile leaves and doesn't start developing adult foliage until it reaches a height of around 2 m, above the browse zone. Breaking off the adult foliage to simulate browsing can apparently induce a reversion to juvenile form.

Henry also described plant adaptations to animal dispersal agents. He said that fruits that are dispersed by birds tend to have a laxative effect, so that they are passed rapidly through the gut and dropped before the bird has flown too far away. Indeed, anyone who has hung out washing near a fruiting elder will know that ripe elderberries pass very rapidly through local birds. In contrast, fruits that are dispersed by slower-moving animals tend to exert a binding effect. For example, the seeds of the endemic Galápagos tomato, *Lycopersicon cheesmanii*, take several weeks to pass through the gut of the Galápagos tortoise. It made me wonder whether any New Zealand plants have developed special adaptations to seed dispersal by flightless birds.

The Beak of the Finch

Our generous hosts in Princeton were Rosemary and Peter Grant, who have been doing research on the evolution of Darwin's finches in the Galápagos Islands for over 27 years. They told us something about the radial evolution of the prickly pear cactus, *Opuntia* spp, there. On islands where the finches nest in the cacti and are important pollinators, the spines are much softer than on islands where the cacti are insect-pollinated and heavily browsed. A Pulitzer prize-winning book, '*The Beak of the Finch*' by Jonathan Weiner, has been written about the Grants' work, which is so meticulous that they have actually been able to document evolution as it happens. Reading this book was one of the highlights of our trip, filling in the gaps, as it did, between Darwin's theory of evolution (itself inspired in part by the curious adaptations of the Galápagos finches) and the current state of knowledge.

One striking example of co-evolution that the Grants have recorded involves changes in the size of the *Tribulus* (puncture vine) seed as the size of the finches' beak changes. This seed is very hard, prickly and relatively large. In times of plenty it is an inefficient means of sustenance, but in times of drought being able to crack it can mean the difference between life and death. In one particularly dry season only the finches with the largest and strongest beaks survived, and nearly all the *Tribulus* seeds were eaten. As the size of the finch beaks has evolved, so has the size of the *Tribulus* seed. But on islands where there are no large-beaked finches the *Tribulus* seed has not increased in size, even though all the plants have suffered the same stressful climatic conditions.

From South America to the Galápagos Islands

So my head was buzzing with new ideas by the time we flew from Quito to the Galápagos Islands, which straddle the equator some 960 km west of Ecuador, the nearest land. There are 14 main islands and over 40 smaller ones. The oldest islands, to the east, are around 5 million years old, and the youngest, to the west and still very active, volcanically, are around 1 million years old, which is very young, in geological and in evolutionary terms. The volcanic origin of the islands means that they have been, and continue to be, thrust up molten from the sea floor as an eastward moving tectonic plate passes over a hot-spot in the earth's mantle.

So how did these remote, oceanic islands come to be populated by a thought-provoking array of plants and animals? When Charles Darwin first set eyes on them in 1835, at the age of 26, the current thinking was that God had created the earth and all the plants and animals on it, and that species, as well as land-forms, were immutable. What we now see as adaptation and co-evolution, the Christian world then saw as examples of the many marvels of creation, such as an extra-long proboscis on a moth so ideally suited to suck nectar from and to pollinate a flower possessing an extra-long nectar tube.

Darwin the Heretic and Experimenter

So what did Darwin see that made him start to think the heretical new thoughts that have so changed the way we see the world? He saw a group of volcanic islands, the youngest of which were so new and sterile that they consisted of little more than raw lava and ash. He saw plants and animals which were strikingly similar to, yet curiously different from, the plants and animals on the nearest landmass, South America, and which also varied from island to island. He began to wonder if the original inhabitants of the Galápagos had arrived from Ecuador, and not by divine intervention, and if, once they had arrived, they had undergone changes.

When Darwin got back to Britain he devoted the rest of his life to testing these new ideas. While animal genera which had undergone adaptive radiation of species, such as finches and tortoises, provided the initial stimulus, it was experiments with plants that provided much of the key evidence for his controversial book, *The Origin of Species by Means of Natural Selection*, which was published in 1859. Darwin reasoned that if the plants and animals on the Galápagos had arrived there by natural means, and evolved into new species there, rather than being created there by God, it was important to demonstrate how this might happen.

Darwin did many thoughtful experiments on plant dispersal (Allan, 1977). He soaked seeds in seawater, to see how long they could be immersed and stay viable. He noted that the seed in the crop of birds was not subjected to gastric juices, and stayed viable for many hours. He calculated how far a bird could fly or be taken in a storm, perhaps to be washed up dying, or torn up by a bird of prey, thus dispersing seeds to a far island. He also fed grain to mice, then fed the mice to hawks and owls in the zoo, and noted how long it took for seed to appear in the predators' pellets, and how viable it was.

A Disharmonic Flora

Around 20,000 plant species exist on mainland Ecuador, from where 90% of the plants on the Galápagos are thought to have originated. Not all species would be capable of surviving long-distance dispersal over 1000km of ocean. Also, some families of plants are better suited for such travel than others. Thus the Galápagos flora is species poor, having between 600 (Jackson, 2001) and 863 (McMullen, 1999) native vascular plants, with around 28 – 30% being endemic. There is also considerable disharmony, or disproportional representation, in the plant families that made it across the sea, compared with Ecuador. Lichens and ferns, for instance, with their tiny, wind-blown spores, and grasses, with their bird-eaten seeds, are over-represented in the islands, while orchids, which have very light seeds, but often require the presence of specific root-associating fungi and specialised pollinators, are under-represented. Gymnosperms, with their heavy cones, never got there at all.

[For those sceptical that even several hundred plant species could have survived such a long and perilous ocean journey, then taken hold and reproduced on such a sterile volcanic substrate, Porter has calculated that it would only take one colonisation every 7,300-12,100 years to account for the ancestors of all the native Galápagos species (McMullen, 1999). That could be one rare combination of flood and gale and currents carrying across a raft of debris with clinging plants and animals. We saw such rafts of broken off riverbank heading out to sea as we flew over the flooded Guayaquil River.]

Toothless Browsers – like New Zealand

Likewise the land-dwelling fauna of the Galápagos Islands are species poor and disharmonic. The only native land-dwelling mammals are bats and the island-specific rice rats. (Darwin was astute enough to note that bats, like birds, could be blown across the sea to distant islands.) But there are 11 subspecies of giant tortoise, 7 species of lava lizard, 6 of gecko and, of course, 13 species of the famous little finch. There are few native butterflies or bees to pollinate the flowers, which are mainly white or yellow. Having fewer species, and disharmonic representation of families, has opened the way for species to forge new relationships and exploit new niches.

On the Galápagos Islands, as with pre-human New Zealand, evolution of the endemic plants has occurred in the presence of large, toothless browsers, and in the absence of any browsing mammals. The biota also evolved, until relatively recently, in the absence of humans; the first recorded visitor being the bishop of Panama in 1535, when his ship was blown off-course in a storm. He survived to tell the tale by sucking the juice of prickly pear cacti. Early sailors who visited reported that the giant tortoises were so numerous that it would be possible to cross some islands without touching the ground, by stepping on their backs. The browsing pressure must have been intense.

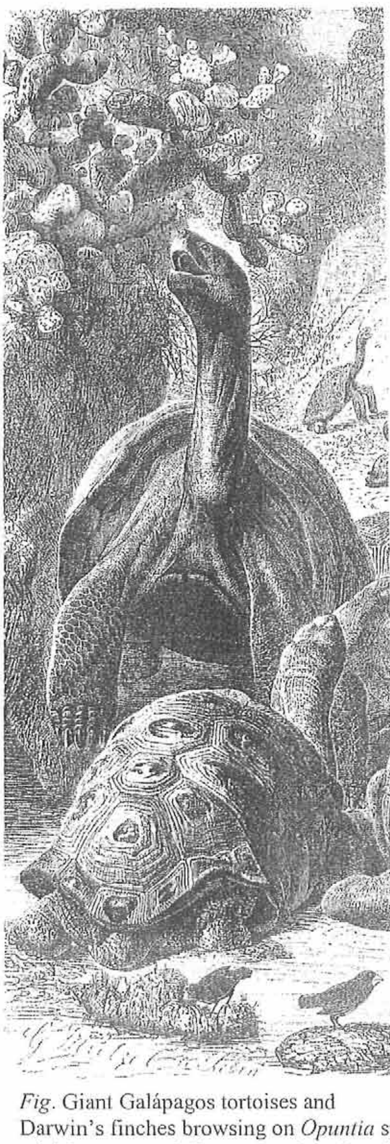


Fig. Giant Galápagos tortoises and Darwin's finches browsing on *Opuntia* sp. prickly pear cacti. *Darwin and the Beagle* by Alan Moorehead, Penguin 1971.

On our visit to the Galápagos, the first toothless browsers that greeted us, as the dinghy from the ex-research vessel Beagle III nudged onto a rocky shore, were the bright red Sally Lightfoot crabs. They pranced boldly round the inter-tidal zone, clipping the bright green seaweed, *Ulva lobata*, with their front nippers, and were a familiar, fearless sight on most islands. After a few days I began to wonder why we never saw any small red crabs, until I learnt that the cryptically-coloured dull grey crabs, that scuttled fearfully away from the stalking rock herons and circling frigate birds, were in fact the juvenile form. The red colour only develops when the crab becomes too big to be easily swallowed.

Competing with the crabs for grazing rights on the seaweed were the amazing marine iguanas. These big, black 'imps of darkness', as Darwin called them, lie basking on the rocks, absorbing heat before and after their forays down to the water to graze on the seaweed, rubbing it off the rocks with their stubby, horny snouts.

On islands where the red algal turf, comprising genera such as *Centroceras*, *Gelidium* and *Spermothamnion*, is grazed, the iguanas have a reddish tinge from the pigment they ingest. Constant grazing by crabs, iguanas, turtles and other creatures keeps the seaweed so well cropped that Darwin thought the marine iguanas must dive off shore for food. In fact the intertidal algae have an exceptionally high rate of growth, and are known to double their length and increase their weight by up to six times in the space of a fortnight (Jackson, 2001).

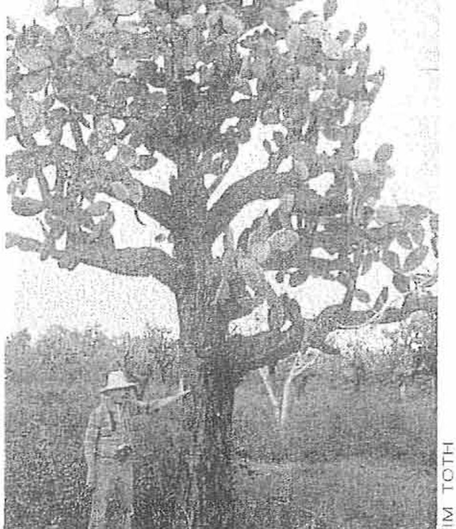
The Plants are Still Evolving

The high rate of endemism in the Galápagos flora indicates a high rate of evolution, and the discrepancy between estimates of number of species is in part because the flora is still evolving. In the relatively short time, geologically, that the Galápagos Islands have been colonised, 18 plant groups have undergone extensive adaptive radiation. The genus with the highest number of endemics is the *Scalesia* daisy, with 16 taxa. Michael Jackson describes this genus as 'the plant kingdom's equivalent of Darwin's finches' Unfortunately, these palatable plants, from the same family as the sunflower, evolved in the absence of browsing mammals. The introduction of burros, horses, cattle and goats in particular has driven some species of *Scalesia* to the verge of extinction, and put others in the rare and threatened category. Staff and volunteers at the Darwin Research station, on Santa Cruz Island, are working hard to save the remaining *Scalesia*.

The next most extensive example of adaptive radiation is in the genus *Opuntia*, in the family *Cactaceae*, where there are 14 endemic taxa. On islands where the *Opuntia* cacti are (or were) browsed by the toothless giant tortoises the cacti have developed an amazing thick trunk, which lifts the fleshy pads above tortoise-browsing level. On islands where there have never been tortoises, and the main browsers are the large land iguanas, the trunks are thicker and shorter, just enough to lift the succulents pads above the iguanas. And on islands where there have never been large reptilian browsers the *Opuntia* just sprawl on the ground as in their ancestral form. In this situation the *Opuntia* tend to reproduce mainly by vegetative means, with new plants sprouting from fallen pads. But on islands where browsing pressure is high, reproduction is mainly by seed.

Fig. Island-specific *Opuntia* sp cacti (Jackson 2001)

Shrubby prickly pear cactus, North Seymour



Giant prickly pear cactus, Santa Fé Island.

Each Island a Petri Dish

That is the most amazing thing about the Galápagos Islands, the variation in species, and in combinations of species, from island to island. Each island is like a little Petri dish, all in the same equatorial ocean incubator, yet each seeded with a different combination of related, yet subtly differing, organisms. Several have, or had, giant tortoises, but the sub-species are largely island specific. Many have, or had, land iguanas, as well as or instead of tortoises. Some have neither reptilian browser. Likewise the combinations of finches, of lava lizards, the little rice-rats, as well as of *Scalesia* daises, *Opuntia* cacti and others of the plant genera that have led to the evolution of 3 or more endemic species, tend to be island-specific. This giant evolutionary experiment is ongoing, greatly accelerated by the arrival of humans. Giant reptiles have been driven extinct on some islands, and have been introduced to others where the plants evolved in their absence. Browsing mammals have been added and removed in various combinations.

Past Climatic Pressures and Evolution

Climatic effects on the ocean 'incubator' have added their own evolutionary pressures over the last 5 million years. Global temperatures have, on average, become cooler over this time. Periodicity of oscillations between glacial and interglacial states has changed from around 20 thousand years to around 100 thousand years. While glacial climates would not have put ice on the Galápagos Islands, the increased water tied up in ice world-wide would have lowered the sea level, exposing land-bridges between some islands. The climate would have been colder and drier. Grant has shown that significant features of the evolutionary radiation of Darwin's finches correspond approximately with the times of greatest climatic change. (Grant, 2001, Jackson, 2001)

Climatic Stress PLUS Browsing Pressure

Climatic stress producing evolutionary pressure is still a marked feature of the Galápagos ecosystems. In the dry season there is almost no groundwater. Annual rainfall can vary from over 3000 mm in an El Niño driven season, as in 1983, to less than 60 mm in a severe drought year, as in 1985, when 90% or more of individuals in certain plant and animal species died. Grant has also shown that, under present day conditions, when the climatic stress is equal, the addition of browsing stress can be what pushes a plant towards speciation, as with the big-beaked finches foraging on the tough *Tribulus* seeds. This fits with the dramatic, large-trunked *Opuntia* cacti occurring on the islands with the biggest browsers, and the sprawling Opuntia, least changed from the ancestral form, occurring on islands without any large reptilian browsers. It is tempting to speculate that short spines and thorns are more effective defense against the soft palate of mammals than the tough, horny palate of browsing birds and reptiles.

Suddenly, it seemed I had found answer to something that had been puzzling me. Matt McGlone had pointed out that moas had been in New Zealand for around 80 million years, yet divarication had only evolved in around the last 5 million years, during periods of great climatic stress; therefore he felt that climatic stress was more implicated than browsing stress. Yet what the Galápagos experiments of nature show quite clearly is that it is the combination of climatic stress PLUS browsing stress that pushes evolution the fastest. Neither alone is as effective. The seaweeds on the Galápagos shores are exceptionally highly grazed, but are not subjected to as much climatic stress as the land plants, and have not become endemic. Neither have the mangroves nor most other unpalatable native plants, which have suffered the same extreme climatic pressures as *Opuntia* and *Scalesia*, but have escaped the heavy grazing.

Insight for the future

A recent Insight Review article by MD Rausher in Nature begins with the sentence "Co-evolution between plants and their natural enemies is generally believed to have generated much of the Earth's biological diversity". The Galápagos Islands are a living demonstration of this, with the added factors of climatic stress and geographical isolation thrown in to make them an evolutionary hot-spot.

What can New Zealand learn from this? It seems to me that Matt McGlone and William Bond could well both be partly right; that climatic stress AND toothless browsers were both important factors in the evolution of our endemic flora. Perhaps it is time they shook hands and collaborated and constructed a more balanced scenario. It could have important implications for the management of our conservation areas.

P.S. Lichens are fascinating – evolution in the making is riveting.

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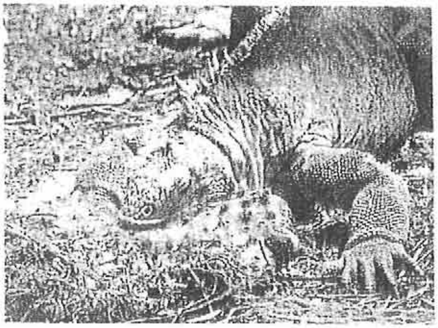

Fig. Land iguana eating prickly pear cactus pad. (Jackson 2001)

REPORTS

Meeting Reports

The last three meetings have continued the wide-ranging theme of botany outside Otago, with 3 splendid and very different talks: Alan Mark on his seven weeks with local ecologists in Tibet, Mongolia and the Russian Caucasus Mountains; Barbara Anderson on the plants she met on her journey through Patagonia, and Sue Benettt on the weeding of the steep, volcanic slopes of Raoul island, the northern-most piece of New Zealand territory. If you didn't go you missed some very interesting talks and colourful slides full of exotic, mind-broadening botany.