claw tree had grown into an impenetrable thicket of small trees, shrubs, and ground level plants. The number of species had also considerably increased. Only photographs of its former state could show us how startling the regrowth of vegetation had actually been (Figs. 1 and 2). One new quadrat was established in the bracken fern (*Pteridium*) zone at the very summit where it adjoined the *Zanthoxylum* zone, to permit determination in the future whether this bracken zone was a permanent feature or whether it would be encroached upon or colonized by elements from the *Zanthoxylum* forest zone.

The final day's work consisted in rechecking the growth, death, and replacement of trees in another vegetation plot in the palo santo (*Bursera*) zone (125 m above sea level) on the lower southeastern slopes. Again as at other plots, it was obvious that rapid regrowth of all species was taking place in the absence of goats. Here the study was extended to include measurements of *Scalesia*, *Bursera*, and *Opuntia* cactus outside the vegetation plot so as to be able to monitor the changes in the population structure in the years ahead. Similar measurements were taken of these species at a lower elevation (45 m above sea level). It was obvious that the plant populations consisted of either very old, large trees or lots of very young trees (which had grown in the absence of goat grazing). Obviously, the trees that should have been intermediate in size had all been eliminated earlier by goats. While doing the work, the team was closely watched by a family of Galápagos hawks, which sat in the low trees above us—almost at arm's reach.

The goat extermination campaign by the Park and Station, though expensive, has been a spectacular success with rapid vegetation regeneration and reestablishment on the west and southern slopes of Pinta (the other parts of the Island are mainly lava fields without vegetation). The team saw no visible signs of goats, but a few goats still remain (a crew member from our boat may have heard one near the western anchorage). Eradication of these few remaining individuals will be difficult and expensive, but it must be done to prevent the population from recovering the high population levels that were so deleterious for the Island. At middle elevations, we encountered several characteristic areas, where dense, forestlike vegetation was interspersed with open, grassy meadows. We considered these areas to be the prime tortoise habitat on Pinta, but sadly we did not find traces of the Pinta tortoise. It appears that Lonesome George will still be lonesome; no mate is available for this sole survivor of the Pinta tortoise population.

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THE SLOW RECOVERY OF *OPUNTIA MEGASPERMA* ON ESPAÑOLA

By: P.R. Grant and B.R. Grant

The mature *Opuntia* cacti of Española have sturdy trunks that support numerous pads from lateral branches. Conspicuous as individuals, they are also conspicuously rare. The best guess as to why they are so scarce is that goats have damaged many old trees and eaten, trampled, or pushed over many of the younger ones. This was the view of Stewart (1911, 1915) who warned that the cactus was in danger of becoming extinct. For example, the density of mature cactus is much higher on the neighboring Island of Gardner which has never had goats. There is no obvious climatic or edaphic difference between the Islands that would account for the difference in cactus density. A parallel situation exists on Floreana (goats common, cactus very rare) and its two satellite Islands, Champion and Gardner (no goats, cactus dense).

Goats were introduced to Española some time in the last century. By the time the California Academy of Sciences expedition visited the Island in 1905-06 the goats were already well established and *Opuntia* were scarce (Stewart 1911, 1915; Slevin 1931). Goats

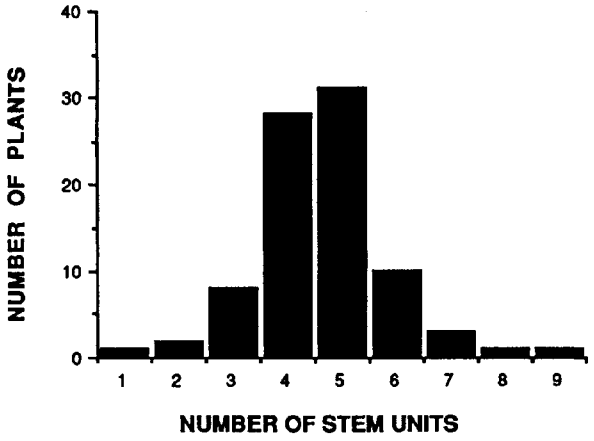

Figure 1. The number of plants observed in each size class as measured by counting stem units on Española in 1979. *El número de plantas en catagorias de tamaño determinado por el número de segmentos en sus truncos, Isla Española, 1979.*

were removed by hunting by 1978 (Hoeck 1984). This should have resulted in good survival of young plants if goats had previously been destroying them. We visited the Island in August 1979, and our observations suggested that indeed *Opuntia* recruitment was well underway.

We attempted to count all young individuals on the top of Red Hill, in an area of approximately 10,000 m^2. The hill is between 0.5 and 1.0 km inland behind Gardner Bay. To characterize the size of the young plants, we counted the number of units in the stem which are demarcated by constrictions.

Altogether we found 85 unbranched saplings, ranging from 1 to 9 stem units, with a mean of 4.6 ± 1.24 (SD) and a mode of 5 units (Fig. 1). If 1 stem is added each year, and growth starts in the year after the seeds are formed, the years of greatest production would have been 1973 and 1974. Heavy rains fell in 1972 and 1973, but not in 1974. According to our observations on Genovesa, Daphne Major, and Champion, seed germination is promoted by wet conditions, so we are inclined to think that the modal class of 5 stem units was 7 years old in 1979. Regardless of the exact ages, a strong production of young *Opuntia* saplings coincided with both heavy rains in the early 1970s and the removal of the last goats.

In addition to the 85 unbranched saplings, one was found with three lateral pads on the top of a 9-unit stem. Seven more branched ones were found further inland. They ranged from 6 to 10 stem units high, and had from 2 to 10 lateral pads. The most complex form was an 8-stem unit trunk supporting two lateral branches of four pads each, with two more pads at the end of one of them. Unless they had matured more rapidly, these were older by a few years than the unbranched ones on Red Hill. Nevertheless, young saplings made up the vast majority of the recruits, on Red Hill and elsewhere.

We returned to Española in early February 1988, and made the same survey on Red Hill. If goats had been the sole agent inhibiting recruitment prior to the 1970s, the large number of young plants seen in 1979 should have survived well and should have been augmented by many new ones produced in the next few years. Far from being augmented, however, the population of young *Opuntia* was drastically reduced. Despite intensive searching we could find only eight unbranched individuals; 1 had 4 stem units, 1 had 5, 2 had 7, and 4 had 9. In 1979 there had been only one branched sapling, but in 1988 there were 10. The number of stem units ranged from 6 to 9 (mean 8.0 ± 1.33 SD), and the most complex in growth form was about as complex as the most elaborate one found on the Island in 1979.

Clearly recruitment had been poor in the intervening years, and mortality among the saplings had been high. Given the age estimation in 1979 of 7 years for an unbranched plant with 5 stem units, the 10 branched plants in 1988 would have been the remnants of the 85 unbranched ones in 1979. We do not know if this is a normal rate of attrition for *Opuntia* plants elsewhere, but the absence of replacement cohorts was not expected.

The key to understanding the poor performance of *Opuntia* may lie in the extraordinary El Niño event of 1982-83. Probably more rain fell on Española then, as it did on other Islands, than at any other time this century (Grant 1984). Prolific rains did not inhibit flowering on the other Islands we visited in 1983 (Genovesa, Daphne Major, and Champion), and they facilitated germination. But they did contribute to the death of several cactus bushes. Roots rotted in waterlogged soil and the bushes, made heavier by extensive uptake of water, were blown over by strong winds (Grant and Grant 1989). The heavy rains also promoted extensive growth of vines which smothered

whole *Opuntia* bushes on Genovesa and Daphne Major, as a result of which several died (Grant 1986). A second El Niño event in 1987, while not as severe or as long, had similar effects on vines and *Opuntia* bushes (Grant and Grant 1989). On Española, we suspect, the rampant growth of vines and other plants in these 2 years (together with the direct effects of rain) caused the demise of all but the tallest and sturdiest of the saplings that germinated prior to 1979, and smothered almost all those that germinated afterwards. In February 1988 the ground cover of Red Hill was a rich, dense tangle of dead herbs.

These observations show that the goat removal "experiment" has still not produced the expected effect on the cactus population. Either the two recent El Niño events, especially the first, have delayed the expected effect, or other factors not yet identified have been responsible for the weak recruitment and low adult density of *Opuntia megasperma* on Española. Time, and further study, will tell. The observations also highlight our ignorance of population processes in *Opuntia* in general. This could be rectified by a well-designed, long-term investigation at the Charles Darwin Research Station, as well as by continued monitoring on Española and Islands similarly affected by goats such as Santa Fé and Pinta (Hamann 1975).

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