EFFECTS OF THE 1998 EL NIÑO ON DARWIN'S FINCHES ON DAPHNE

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El Niño events are amplifications of normal seasonal processes in the eastern tropical Pacific region (Philander 1990), and they bring an abundance of rain to the Galápagos. Since 1973 we have been studying how populations of Darwin's finches on the small island of Daphne Major respond to conditions that vary from droughts of scarcity to El Niño years of plenty. For us this variation is like a gigantic watering experiment that decreases or increases the food supply of the finches (seeds, caterpillars, spiders, pollen, nectar, etc.) at the normal time of breeding, while leaving other potentially influential factors either unaffected (photoperiod) or affected in a minor way (temperature). The experiment is not under our control, nevertheless we can learn a lot by comparing the responses of finches in different years. The finches in question are four species of *Geospiza* ground finches: large (*G. magnirostris*), medium (*G. fortis*), and small (*G. fuliginosa*) ground finches, and the cactus finch (*G. scandens*).

We have studied finches on the island throughout the entire breeding season in four El Niño years (1982-83, 1987, 1991, and 1998), as well as ten other years of breeding (Grant *et al.*, ms.) and three other years of drought and no breeding (1985, 1988, 1989). Three features of breeding vary among years. They are the number of eggs a female lays in a clutch, the success in raising the young to the point of fledging, and the number of times a female breeds. The sum total of these components is the annual production. Production is on average four times higher in El Niño years than in non-El Niño years. The main reason for the high production is that finches breed four to eight times in El Niño years, instead of the usual one (or none) to four times in non-El Niño years. Clutch sizes are also larger in El Niño years than in non-El Niño years, and fledging success is slightly higher in El Niño years, although hatching success tends to be a little lower in part because the foraging of the parents is interrupted by rain. Remarkably, in the longest breeding seasons of all (1982-83 and 1987), young finches hatched at the beginning of the season were breeding three months later and contributing to the total production; some finches became grandparents within one season!

How did the responses of finches in 1998 compare with responses in other El Niño years? Rainfall on Daphne in 1998 amounted to two-thirds of the quantity that fell in the mega-El Niño of 1982-83. This should have resulted in prolonged and prolific breeding of the finches to an extent exceeded only in 1982-83, but it didn't. A few birds bred in January following the heavy and repeated rains that began in the last few days of 1997. By February breeding was in full swing and continued in March, April, and May, but by the second week of June, breeding had ceased. Thus the start to the breeding season was sluggish, and the end was precipitous, and neither was expected from the pattern of rainfall. For example, rain continued into early June, but finches did not continue to breed. This pattern was seen in all four species.

In two respects finch breeding in 1998 was typical of breeding in a Niño year. First, clutch sizes were distinctly higher than in non-El Niño years; clutches of five eggs were moderately common in 1998, whereas they are exceedingly rare, if they occur at all, in non-El Niño years. The larger number of eggs in a clutch suggests that females find it easier to get enough food to make eggs in Niño years, and 1998 was no exception to the rule. Second, hatching and fledging success were also about the same as in other El Niño years. The anomalously low production in 1998 was clearly brought about by an unexpectedly short breeding season. Why?

More specifically, why did breeding start slowly and end rapidly? Normally, the length of the breeding season appears to be governed by a food supply that is replenished for as long as the rain continues. In 1998, the length of the breeding season was not so clearly determined by the pattern of rainfall, but perhaps the populations of caterpillars took a long time to increase, and then decreased quickly at the end of May. Our previous work on both Daphne and Genovesa (Gibbs and Grant 1987, Grant and Grant 1989) makes this a plausible explanation. However, at best it is only partly correct; although their numbers were declining, caterpillars were still fairly plentiful in our samples in June, when finch breeding had all but ceased.

The explanation may lie instead in a combination of unusual conditions; high initial densities of finches and exceptionally high temperatures. Breeding may have been delayed as a result of much interference. An unknown factor that might have contributed to the delay is a carry-over effect from the extensive breeding in the previous (El Niño) year; finches may not have been physiologically ready to breed when the rains returned at the end of 1997. Breeding ceased early in 1998, perhaps because the energetic benefits gained from a declining food supply was offset by rising energetic costs of nest and territory defense as overall density, adults and fledglings combined, increased. High air temperatures may have contributed to the increase in costs. They were higher than in all previous El Niño years.

Whatever the reasons, patterns of breeding on Daphne are not unique, but are likely to occur in parallel fashion elsewhere on other islands when effects of El Niño conditions are experienced throughout the archipelago. In previous El Niño years, Darwin's finches on two widely separated islands, Genovesa (Grant and Grant 1989) and Daphne Major (Gibbs and Grant 1987), responded in the same way to heavy rain and a prolonged wet season (Grant and Grant 1996). Clutch sizes were elevated and finches bred repeatedly. In 1998, short-term observations of ground finches on other islands indicated repeated breeding, but an early cessation, perhaps even earlier than on Daphne (D. Day, M. Hau, and M. Wikelski, pers. comm.).

One of the things we have learned from this long-term study is that no two El Niño years are alike. An obvious reason for this is the amount of rain and the number of months in which it falls varies among El Niño years. However, this is not the only reason. Responses to El Niño conditions are determined in part by preceding conditions, be they dry or wet, food-rich or food-poor. Those preceding conditions in turn are determined by whether drought or normal conditions precede the Niño perturbation and on the interval since the previous Niño event. For example, finch population densities were much higher at the beginning of 1998 than at the beginning of 1983, and finches probably interfered with each other's attempt to breed at the beginning of 1998. This, we believe, is one reason why finch breeding took so long to get underway in 1998. Thus, effects of El Niño can be fully understood only by placing them in their temporal context. We would never have learned this lesson if the Niño watering experiment had been under our control.

ACKNOWLEDGMENTS

Fieldwork was conducted with permission and support from the Galápagos National Park Service and the Charles Darwin Research Station, Galápagos. Funding has been received from NSERC (Canada) and NSF, most recently BSR-9615383. We thank Solanda Rea at the Charles Darwin Research Station for supplying temperature data, the numerous assistants who have given help in the field, L.F. Keller, K. Petren, E. Monson, and C. Edwards for help in the 1998 season, and G. Estes for reading the rain gauge when we were not on the island.

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EL NIÑO AND INTRODUCED INSECTS IN THE GALÁPAGOS ISLANDS: DIFFERENT DISPERSAL STRATEGIES, SIMILAR EFFECTS

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INTRODUCTION

Oceanic islands are considered fragile ecosystems. The introduction of one or more alien species can often lead to a series of important ecological alterations. Alien species are often able to rapidly colonize oceanic islands in the absence of natural enemies and other biotic factors that, in their native range, maintain population numbers at a natural level. These species often possess characteristics that enable them to occupy a wide variety of niches that have yet to be filled by native species and, in some cases, can displace them (Vitousek 1998).

A 960-km oceanic barrier has isolated the Galapagos Islands from continental America, but recent colonization by humans has increased the introduction of alien species to the islands. Peck *et al.* (1998) have identified 292 introduced insects from the Galápagos Archipelago and it is estimated that there are many more to be found. Accidental transport by humans is the principal cause for these introductions, while a variety of methods is responsible for the distribution of these insects within the Archipelago, including dispersal by air currents. It has long been suspected that the periodic El Niño events contribute to insect dispersal to and within the Archipelago. However, to our knowledge, published information about the impact of these irregular climatic conditions on the behavior and dispersal strategies of alien insects is non-existant.

Six alien insect species are highly aggressive and a threat to the flora and fauna of the Galápagos Islands. In 1997, the Entomology Program of the Charles