ture of late-onset non-insulin-dependent diabates mellitus, it is possible that dysregulation of the HNF regulatory pathway, whether primary or secondary, can also contribute to this complex metabolic syndrome.

References and Notes
10. The HNF-3α targeting vector was constructed by deleting the DNA binding and transcriptional domains between the AffI III and Nhe I sites in exon 2. The E. coli lacZ gene was fused in frame to exon 2 of HNF-3α, which placed it under the control of HNF-3α transcriptional regulatory sequences. Recombinant ES cells were generated by Southern blotting. Genomic DNA was digested with Hind III-Eco RV and blots were probed with HNF-3α genomic DNA, which was hybridized to sequences present in the targeting vector. The wild-type allele produced a 7.5-kb restriction fragment, whereas the targeted allele produced a 4.5-kb fragment. The production of lacZ- and HNF-3α—/— embryos were generated by crossing M.S. and S.A.D. also thank J. Smith and T. Minsa for giving us enthusiasm for science. M.S. is an Irma Hirschl Scholar, Pew Scholar, and Robert and Harriet Heilbrunn Professor. S.A.D. is a Naomi Judd American Liver and an Alexandrine and Alexander Sinzheimer Scholar. M.A.N. was supported by a postdoctoral fellowship of the Spanish Ministry of Education and Culture. D.D. was supported by the Fonds de la Recherche en Sante du Quebec and the National Cancer Institute of Canada (NCIC). J.R. is a NICRY Terry Fox Research Scientist, a Medical Research Council Distinguished Scientist, and a Howard Hughes Medical Institute International Research Scholar. Supported in part by the American Diabetes Association and by the March of Dimes.

Impact of a Catastrophic Hurricane on Island Populations
David A. Spiller,* Jonathan B. Losos, Thomas W. Schoener

Lizard and spider populations were censused immediately before and after Hurricane Lili on islands differentially affected by the storm surge. The results support three general propositions. First, the larger organisms, lizards, are more resistant to the immediate impact of moderate disturbance, whereas the more prolific spiders recover faster. Second, extinction risk is related to population size when disturbance is moderate but not when it is catastrophic. Third, after catastrophic disturbance, the recovery rate among different types of organisms is related to dispersal ability. The absence of the poorer dispersers, lizards, from many suitable islands is probably the result of long-lasting effects of catastrophes.

Natural catastrophes such as hurricanes and volcanic eruptions may be so catastrophic that biotas in exposed areas are scarred and even reshaped for years to come. Although major disturbances are potentially of such great importance (1), few precise field data are available to evaluate their impact. Reliable information on the biota before the disturbance is often absent, as is the case for the most lengthily monitored major disturbance of all, the eruption of Krakatoa’s volcano in 1883 (2). Furthermore, because major disturbances are rare, the initial impact and the incipient stage of recovery are often missed because of the low probability of scientists being in just the right place at the right time.

In October of 1996, the highly improbable happened. We had just finished a census of lizard and spider populations on 19 islands (Fig. 1) near Great Exuma, Bahamas, as part of a long-term experimental study of the ecological effects of introducing two lizard species (Anolis sagrei and A. carolinensis) (3, 4). Vegetation profiles of each island, which were protected from this aspect of the hurricane. The next day, as soon as the storm subsided, and for 3 days thereafter, we recensused populations on all the islands. All populations were again censused about 1 year later (23 to 28 September 1997).

These unique data allow us to evaluate several propositions concerning the impact of disturbances on different types of organisms. First, that larger organisms may be more resistant than smaller ones to the immediate impact of a moderate disturbance (8, 9). Second, that surviving smaller species may recover faster because their reproductive rate is higher than that of larger species (9). Third, that for moderate disturbances, the risk of extinction is a function of population size, whereas no such relationship exists for catastrophic disturbances (10). Fourth, that when all populations are exterminated by a catastrophic disturbance, the recovery rates of different species will be largely determined by their dispersal abilities (11). To evaluate...
these propositions, we compared the effect of the hurricane on lizards versus spiders and on protected versus exposed islands.

On the protected side, although effects were marked, a moderate number of individuals survived: The mean number of lizard individuals per island was 34% lower immediately after than before the hurricane, whereas the mean number of web-spider individuals was 79% lower (Fig. 2A). The change was statistically significant for lizards ($P = 0.044$) and for spiders ($P = 0.002$) and was significantly greater for spiders than for lizards ($P = 0.032$) (12). The mean number of web-spider species was reduced ($P = 0.040$), but the number of lizard species remained constant (Fig. 2B). Comparisons between censuses immediately after and 1 year after the hurricane showed that the numbers of lizard individuals were not significantly different ($P = 0.401$), whereas the number of spider individuals ($P = 0.005$) and species ($P = 0.025$) had increased. Thus, the data show that the larger lizards were more resistant to the immediate impact of the moderate disturbance on the protected side, which is in accordance with the first proposition above. Lizards may have been able to withstand the physical forces of the disturbance or to find protective cover better than spiders. On the other hand, spiders, which are generally more fecund and have shorter generation times, recovered faster than lizards, which is in accordance with the second proposition.

On the exposed side, all lizard and spider populations were exterminated (Fig. 2C). On 6 of the 11 islands, a few spider individuals were found immediately after the hurricane but these belonged to $Metazygia bahama$, a species completely absent on all the islands before the hurricane (13); spiders sustained a net 97% loss in total numbers ($P = 0.001$). One year later, no lizard was found on the study islands. In contrast, the numbers of spider individuals and species were higher the year after than immediately after the hurricane ($P = 0.011$ for individuals; $P = 0.014$ for species) (Fig. 2, C and D).

Figure 3 shows the numbers of individuals (population size) of each species recorded on each island before the hurricane that were determined as extinct and extant immediately after. On the protected side, none of the five introduced lizard populations became extinct, even though two populations were very small (fewer than five individuals). In addition to the introduced populations, the presence of natural lizard populations ($A. sagrei$) was ascertained before the hurricane on five small islands on the protected side (4); no such population became extinct. In contrast, 9 of 22 web-spider populations became extinct. The proportion of populations becoming extinct was significantly higher for spiders than for the introduced and natural lizard populations combined ($P = 0.018$; Fisher’s exact test, one-tailed), which again supports the first proposition. Spider populations becoming extinct were significantly smaller than those remaining extant ($P = 0.032$) (12).

![Fig. 1.](image1.png)  (A) Map of the central region of the Bahamas showing the path of Hurricane Lili. (B) Asterisks indicate the locations of the study islands.

![Fig. 2.](image2.png)  Mean numbers of individuals and species of lizards and web spiders on protected (A and B) and exposed (C and D) islands immediately before (9 to 17 October 1996; white bars), immediately after (20 to 23 October 1996; black bars), and 1 year after (23 to 28 September 1997; gray bars) Hurricane Lili. Error bars indicate standard errors.

![Fig. 3.](image3.png)  Relationship between population size recorded immediately before and extinctions recorded immediately after Hurricane Lili for each species of lizard and web spider on protected and exposed islands.
On the exposed side, all lizards and spiders became extinct even though the population sizes of some were large; the maximum lizard and spider populations had 186 and 143 individuals, respectively. In addition, all of the five natural lizard populations (A. sagrei) we found before the hurricane on small exposed islands also became extinct. This extinction versus population-size relationship was used by Pimm et al. (10) to characterize “catastrophic” extinction, but apparently no illustrative data were available until now. Moreover, the results for spiders on the protected and exposed islands, taken together, provide the first precise demonstration of the third proposition.

What feature of the hurricane was responsible for the catastrophic extinction on the exposed islands? Because most of Great Exuma lies below an altitude of 10 m, wind velocity during the hurricane over its protected satellite islands was probably equal to, or only slightly less than, that over its exposed islands. However, Great Exuma did substantially impede the effect of the storm surge on the protected islands—immediately after the hurricane, we observed much scouring by water (for example, erosion and sand deposition) even on the highest surfaces of all exposed islands, but no such damage was present on protected islands. Moreover, the volume of vegetation was much more reduced on exposed than on protected islands, averaging 42% (SE = 5.1) versus 15% (SE = 7.1), respectively. Thus, the storm surge appeared to be the aspect of the hurricane that was responsible for catastrophic extinction on the exposed islands. Similar differential effects of hurricanes were found for corals in protected and exposed areas located on opposite sides of Heron Island on the Great Barrier Reef (15). Other studies of lizards (16) and birds (17) in different areas on very large West Indian islands have also shown substantial differences in hurricane damage. Thus, marked spatial heterogeneity appears to be a common feature of the impact of hurricanes on natural populations.

The results on the exposed islands 1 year after the hurricane are in accordance with the fourth proposition. Although the number of spider individuals averaged about one-third of the prehurricane value, the mean number of spider species reestablished to exactly the same value as before the hurricane. A rapid return to a dynamic species equilibrium (18) is suggested, just as has been found in experimental defaunation studies of collective arthropod biotas on small islands (19). Hence, although hurricanes may exterminate spider populations, many small islands are quickly recolonized, including some without lizards, where spiders can reach extraordinarily high densities (20). The excellent over-water dispersal abilities of such arthropods seems clearly responsible. Indeed, the first known colonist of the denuded Krakatoa was a spider (21). In contrast to spiders, recolonization by lizards was minimal (21). Bahamas lizards have been experimentally introduced, repeatedly and successfully, onto small islands where they do not naturally occur (22, 23). Because these islands were united with much larger ones when sea levels were lower 8000 to 10,000 years ago (24), it is reasonable to conclude that they did at one time have lizard populations. This suggested to us (22) that infrequent catastrophic hurricanes exterminated lizards on such islands. We now have an actual demonstration of the hypothesized mechanism. Immediately after the hurricane, lizards were found on a large exposed island, but only in the highest area. Hence, catastrophic extinction of lizards may have occurred only on islands small enough to be inundated completely during the hurricane. Thus, given the poor dispersal abilities of lizards, their absence from most small islands may literally represent the high-water mark of previous hurricanes. More generally, this study suggests that after a catastrophic disturbance, the recovery rate among different types of organisms increases strongly with dispersal ability.

References and Notes
3. The experiment was designed to measure colonization success of and the effect of interactions between the lizard species represented in (4). Briefly, in October 1993 and 1994, lizards were introduced onto 15 islands. The vegetated area of the islands ranged from 203 to 1511 m². Lizard population sizes were usually estimated by means of the multiple mark-recapture method [S. H. Fienberg, Biometrika 59, 591 (1972); D. G. Heckel and J. Roughgarden, Ecology 60, 816 (1979)]. Islands were marked with different colors of nontoxic paint on each of 3 paint. On a few occasions, lizards were marked on only 2 days, and the Lincoln index was used to estimate population sizes. We searched the entire island for web spiders, recording the species identity of all observed individuals on each of the lizard-introductions islands and on four islands without lizards.
5. Vegetation volume was estimated before (October 1994) and after (December 1996) the hurricane on each island as follows. Each island was approximated as an ellipse. A measuring tape was placed along the major axis of the island, from the beginning to the end of the vegetation. Perpendicular transects were placed at 4-m intervals on larger islands and at 3-m intervals on smaller islands. The maximum height of the vegetation within a 0.5-m radius of a given point was measured along each transect, at 3-m intervals on larger islands and at 2-m intervals on smaller islands. The area was estimated by constructing the outline of transects and measuring the enclosed area. Volume was estimated by multiplying mean maximum vegetation height by vegetated area.
12. The proportional changes in numbers of lizards and spiders between two censuses on each island were shown to be statistically greater than zero by performance of a paired t test on log-transformed numbers. The P values are one-tailed because numbers were expected to decrease from immediately before to immediately after the hurricane. The difference between lizards and spiders in the proportional change was analyzed with a t test; the P value is one-tailed because the numbers of spiders were expected to decrease from immediately after the hurricane. The P values for changes from immediately after versus 1 year after the hurricane are two-tailed.
13. This surprising observation suggests that the hurricane transported the spiders over a much larger area than expected. Although these spiders might have come from Great Exuma, M. bahama was previously recorded on only Andros and Bimini, located 100 km from the study islands [H. W. Levi, Bull. Mus. Comp. Zool. 154, 81 (1995); H. Levi, personal communication]. One year after the hurricane, M. bahama was absent on all islands, as it was in each of our four annual censuses before the hurricane.
21. No lizard species recolonized any of the 11 exposed islands having introduced lizard populations. One small exposed island having a natural lizard population before the hurricane was apparently recolonized; no lizard was found immediately after the hurricane but a few were found the next year. This island was very close (~30 m) to a much larger island and was the nearest to Great Exuma of all the islands surveyed. On the four other small exposed islands surveyed that had natural lizard populations before the hurricane, no lizard was found immediately after nor 1 year after the hurricane.
25. We thank R. Mayfield for field assistance, H. Levi for spider identifications, and NSF for support.
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