## Genes Record a Prehistoric Volcano Eruption in the Galápagos

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Volcanic islands provide notable examples of the parallel between a changing geographic area and its changing biota. This is particularly true for young islands where volcanic activity is known to dictate the rate of population extinction and recolonization and to influence evolutionary diversification (1). However, examples of demographic changes associated with historical volcanism are hard to describe because of difficulties in extracting information about population history. Here, we show that genes of a giant tortoise population have recorded a signature associated with a sizable prehistoric eruption of Volcano Alcedo on the Galápagos Islands.

Alcedo is located on Isabela, an island with five giant tortoise taxa occupying each of its five major volcanoes (2). The Alcedo taxon (Geochelone nigra vandenburghi) is a genetically differentiated population found in vegetated areas of the volcano (3-5). A large-scale mitochondrial DNA (mtDNA) survey (3) surprisingly revealed that vandenburghi, the largest population of tortoises in the archipelago with about 3000 to 5000 individuals (6), has three to five times less matrilineal diversity than the other four Isabela taxa. Reduced genetic diversity seems incompatible with young population age because Alcedo emerged above sea level at about the same time as the other Isabela volcanoes  $[\sim 500,000 \text{ years ago } (500 \text{ ka})](7)$ . Additionally, Alcedo was probably never exploited by whalers who caused reductions of tortoise populations on more accessible islands (2). However, Alcedo is unique amongst Galápagos volcanoes because it experienced a major explosive eruption in prehistoric times (7); otherwise, Galápagos volcanoes are constructed of basaltic lavas that erupted by nonexplosive effusion. The major Alcedo eruption deposited

>3.4 km<sup>3</sup> of rhyolitic tephra onto itself. Two K-Ar age determinations on coeval rhyolitic lavas are 74,000 and 120,000 years (7). The interpretation based on these dates and stratigraphic constraints is that the eruption was about 100 ka (7). We propose that this eruption,

which covered most of the prime tortoise habitat with meters of hot pumice, caused a dramatic population reduction and that *G. n. vandenburghi* is currently derived from an abundant lineage that survived this catastrophe.



**Fig. 1.** Inset shows the Galápagos Islands; enlarged view of Isabela Island shows three volcanoes from central and southern regions. Summary of results are presented together with haplotype networks. Approximate distribution of populations are shown in green (Volcano Alcedo), blue (V. Sierra Negra), and yellow lines (V. Cerro Azul). Dotted black lines represent distribution of other populations. *h*, mtDNA diversity; *A*, microsatellite diversity; *n*, sample size. Numbers for Alcedo haplotypes (61 to 65) correspond to numbers in GenBank. White asterisks indicate populations where haplotype 61 is also found. Size of the ovals in network diagram is proportional to haplotype frequency in each population. Line between haplotypes that we did not sample or went extinct.

This hypothesis was tested by analyzing genetic variation at 10 nuclear microsatellite loci and 700 base pairs of the mtDNA control region in *G. n. vandenburghi* and in populations of *G. n. guntheri* and *G. n. vicina* (8). The Alcedo population has less microsatellite (P <

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0.01) and mtDNA diversities (91% of tortoises share the same maternal lineage) than other populations. A test for bottleneck based on heterozygosity excess suggests past population contraction in *G. n. vandenburghi* (Fig. 1), a result corroborated by the M ratio test (8).

The time since population contraction can be estimated from G. n. vandenburghi's distinctive mtDNA network, which is composed of abundant and ancestral haplotype 61 (also found in other Isabela populations) and the four recently descended haplotypes 62 to 65 (Fig. 1). Reduced variability is likely due to reinvasion of Alcedo by tortoises with haplotype 61 that survived the eruption. Hence, the geologically estimated time of volcano eruption should predate the coalescence of haplotypes 62 to 65 (the time back to the common ancestor of these haplotypes). We confirmed this prediction using methods that suggest a coalescence of the existing variation of about 88,000 years (72,400 to 118,700 vears) (8). Given that G. n. vandenburghi is genetically (3, 5) and morphologically (2)divergent from southern Isabela populations, our study supports a generalized theory that population contractions influence evolutionary diversification (1). Our results also emphasize the value of modern molecular population approaches in obtaining historical demographic information that cannot be discerned based on contemporary scenarios.

## **References and Notes**

- 1. H. Carson, J. P. Lockwood, E. M. Craddock, Proc. Natl.
- Acad. Sci. U.S.A. 87, 7055 (1990).
  P. C. H. Pritchard, Chelonian Res. Monogr. 1, 1 (1996).
- 3. L. B. Beheregaray *et al.*, in preparation.
- 4. A. Caccone *et al.*, *Evolution* **56**, 2052 (2002).
- 5. C. Ciofi et al., Mol. Ecol. 11, 2265 (2002).
- C. G. MacFarland, J. Villa, B. Toro, *Biol. Conserv.* 6, 118 (1974).
- D. Geist, K. A. Howard, A. M. Jellinek, S. Rayder, Bull. Volcanol. 86, 243 (1994).
- Materials and Methods are available as supporting online material on *Science* Online. Sequence data are deposited with GenBank (accession numbers AF548204 to AF548286).

## Supporting Online Material

www.sciencemag.org/cgi/content/full/302/5642/75/DC1 Materials and Methods References

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