Evidence of Drought-Induced Evolution in the Pinyon Jay (Gymnorhinus cyanocephalus)

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Abstract

In the southwestern United States, climate change has caused severe and prolonged drought. As a result, the pinyon pine (Pinus edulis), has experienced high mortality and reduced productivity. Diminished pinyon seed production might have affected the evolutionary trajectories of other species, such as the pinyon jay (Gymnorhinus cyanocephalus). To investigate whether pinyon jay characteristics evolved as a result of the 2002-03 drought, data on 13 morphological traits and eight microsatellite loci were collected and analyzed for differences in magnitude and distribution before and after the drought. Individuals with traits linked to enhanced physiological capacity and higher social status survived the drought differentially. Allele frequencies at two microsatellite loci changed and population structure decreased during the drought. These results suggest that the drought caused phenotypic and genetic evolution in the pinyon jay and other keystone species could affect ecological and evolutionary dynamics in the pinyon-juniper ecosystem.

Introduction

An increasing body of evidence indicates that the Earth’s climate is warming (IPCC 2001). One possible consequence is the recent series of droughts in the American southwest. The most severe of these occurred in 2002-03 (NOAA 2008). This drought caused the pinyon pine (Pinus edulis) to experience high mortality and decreased productivity (Gillini et al. 2006), which could have affected other keystone species such as the pinyon jay (Gymnorhinus cyanocephalus). The pinyon jay depends on pinyon seeds for overwinter survival and early reproduction (Brown et al. 1990). The drought of 2002-03 may have affected individuals’ abilities to harvest seeds or capitalize on nontraditional foods. Other characteristics such as body size are correlated with social rank (Gillari et al. 2006) and could affect individuals’ access to food (Harter et al. 2006). A second hypothesis suggests that the genetic composition of the flocks changed. Within flocks, gene frequencies could have been affected as phenotypes at various loci were selected for or against. Among flocks, gene flow and population structure could have been affected as dispersal patterns changed. Understanding the evolutionary implications of the 2002-03 drought on the pinyon jay will help us quantify and understand the effects of climate change on other keystone species in the pinyon-juniper woodland. It is important to understand how such species are affected by severe drought, because evolution of keystone species can have cascading ecological effects (Brown et al. 2001).

Methods

To test the hypotheses that phenotypic and genetic factors evolved because of the 2002-03 drought, 637 pinyon jays in three flocks (Cave Crater, and Herardo) were trapped in the vicinity of Flagstaff, Arizona (Figure 1). Data for eight morphological traits (Table 1) and eight microsatellite loci (Busch et al. submitted) were collected from each individual. Data collection occurred for eight years (2000-07), during which time the drought and pinyon pine die off occurred.

The 2002-03 drought caused a significant reduction of the regional pinyon jay population (Wiggins 2005). In this study, individual jays were classified as survivors and non-survivors (NS). Survivorship categories were further subdivided into gender and flock groups for analysis. Morphological traits were aggregated into principal components (PCs). The distribution of each PC was compared between groups using a randomized block test with 10,000 permutations. Distributions of alleles at microsatellite loci were examined using likelihood ratio X² tests. Population structure (SFS) before, during, and after the drought was calculated with RSTCALC (Goodman 1997) and characterized using rho, an unbiased estimator of R². If selection on morphological traits or genetic composition of the flocks occurred, then differences in the distribution of traits between S and NS groups before and after the 2002-03 drought would be evident.

Results

Phenotypic Data

Of the three PCs extracted from the morphometric data, two principal components (PC) accounted for 44.70% of the variation (Eigenvalue = 5.81) and characterized traits associated with physiological capacity (flight feather lengths, body mass, and bill length). PC2 accounted for 16.71% of the variation (Eigenvalue = 2.17) and characterized traits associated with social status (bill, body, and bill size).

Table 2. Primary traits in each principal component.

Survivors had larger values for both PC1 (n=106, mean = 141, t = -2.45, p = 0.01) and PC2 (n=106, mean = 141, t = -1.75, p = 0.08) than did the non-survivors in the whole population (Figure 2). Differences in PC1 were most evident in the Cosimo flock (n=21, mean = 95, t = -1.90, p = 0.06). Differences in PC2 were most evident in the Herald Ranch flock (n=72, mean = 75, t = 1.75, p = 0.08).

Genotypic Data

Six and seven groups had different distributions at alleles at two microsatellite loci: AAAG9 (n=157, mean = 366, X² = 14.79, p = 0.06) and GATA4 (n=301). At AAAG9, differences were more evident among males (n=102, mean = 166, X² = 21.9, p = 0.01; Figure 3). At GATA4, differences were more evident in the Cosimo flock (n=48, mean = 310, X² = 6.91, p = 0.02; Figure 4).

Average rho was higher before (average rho = 0.06) than during the drought (average rho = 0.00) (Figure 5).

Discussion

Evidence suggests that both phenotypic and genotypic traits evolved because of the 2002-03 drought. Individuals with traits associated with greater physiological capacity and social status survived the drought differentially. Birds with greater physiological capacity might have had a greater ability to survive food shortages, temperature extremes, metabolic demands of increased dispersal, and physical demands of foraging over wide areas. Birds with higher social status might have had a greater ability to dominate food resources (e.g. Harter et al. 2006). Some loci, such as microsatellite loci also survived the drought differentially. Alleles could have changed in frequency as a result of genetic drift, or because they were subject to natural selection. While the loci examined in this study are non-coding (Busch et al. submitted, Benford et al. 2006), they could be linked to selectively important genes.

Population structure decreased during the drought. Dispersal from food-poor areas to food-rich areas might have increased, resulting in an admixture of flocks. Evolutionary changes in the pinyon jay could affect other species in the pinyon-juniper ecosystem. While this study provides a promising starting point, investigation of both short-term effects of the 2002-03 drought and the resulting population bottleneck in keystone and ancillary species is necessary.

References

Busch, H.C. 1959. The elimination of the unit cell as illustrated by the Inverted House Sparrow. Peabody Museum, Biological Laboratory, Mount Holyoke College, Whittier Hall.

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Table 1 (above). Morphological measurements taken on each bird. Weight is given in all other measurements in mm.

Table 2. Primary traits in each principal component.

Figure 1 (left). Three focal flocks of pinyon jays near Flagstaff, Arizona.

Figure 2. Differences in average PC1 (n=195, mean = 141, t = 1.75, p = 0.08) and PC2 (n=195, mean = 141, t = 1.75, p = 0.08) values for survivors versus non-survivors. Error bars represent ±SE.

Figure 3. Allele frequencies of allelic 207, 215, 219 a 238 at AAAG9 for non-survivors and survivors.

Figure 4. Frequencies of allelic 217, 221, 225 and 233 at GATA4 for non-survivors and survivors.

Figure 5. Average rho values before (0.02) and after (0.00) the drought.