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 genotypic evolution in the pinyon jay. Evolution of 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 (Gitlin *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 (Balda 2002, Marzluff and Balda 1992). It would therefore be valuable to know what the evolutionary implications of the drought-induced seed shortage on the pinyon jay might have been.

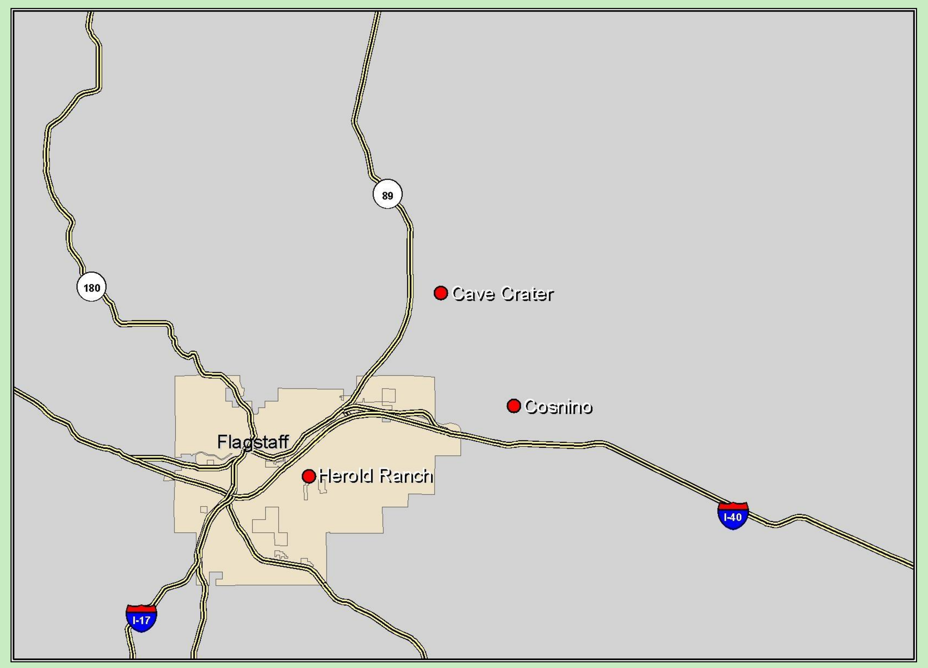
One hypothesis suggests that morphological features associated with the exploitation of food resources changed (*e.g.* Boag and Grant 1981, Bumpus 1899). Some physical characteristics such as bill size could affect individuals' abilities to harvest seeds or capitalize on nontraditional foods. Other characteristics such as body and bib size are correlated with social rank (Strasser *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 genotypic features evolved because of the 2002-03 drought, 637 pinyon jays in three flocks (Cave Crater, Cosnino, and Herold Ranch) were trapped in the vicinity of Flagstaff, Arizona (Figure 1). Data on 13 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.



Right Primary 10	Left Primary 10
Right Primary 9	Left Primary 9
Right Outer Tail	Left Outer Tail
Upper Mandible	Lower Mandible
Bill Depth	Bill Width
Bib Width	Bib Length
Weight	

Table 1 (above). Morphological measurements taken for each bird. Weight in g; all other measurements in mm.

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

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 (S) 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 t-test with 10,000 iterations.

Distributions of alleles at microsatellite loci were examined using likelihood ratio X^2 tests. Population structure (R_{ST}) before, during, and after the drought was calculated with RSTCALC (Goodman 1997) and characterized using rho, an unbiased estimator of R_{ST}.

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 predominated (Table 2). PC1 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 (bib, body and bill size).

Principal Component 1: Traits Associated with Physiological Capacity		**Principal Component 2: Traits Associated with Social Status**	
Character	**Eigenvector**	**Character**	**Eigenvector**
Left Primary 9	0.11	Bib Length	0.48
Right Primary 9	0.11	Bib Width	0.45
Left Outer Tail	0.10	Right Primary 10	-0.33
Right Outer Tail	0.10	Left Primary 10	-0.33
Right Primary 10	0.09	Weight	0.30

Table 2. Primary traits in each principal component.

Survivors had larger values for both PC1 (n_S = 106, n_{NS} = 141, t = -2.45, p = 0.01) and PC2 (n_S = 106, n_{NS} = 141, t = -1.75, p = 0.08) than did non-survivors in the whole population (Figure 2). Differences in PC1 were most evident in the Cosnino flock (n_S = 21, n_{NS} = 95, t = -1.90, p = 0.06). Differences in PC2 were most evident in the Herold Ranch flock (n_S = 72, n_{NS}= 25, t = -1.757, p = 0.08).

Genotypic Data

S and NS groups had different distributions of alleles at two microsatellite loci: AAAG9 (n_S = 157, n_{NS} = 366, X^2 = 14.79, p = 0.06) and GATA4 (p = 0.31). At AAAG9, differences were more evident among males (n_S = 102, n_{NS} = 166, X^2 = 19.56, p = 0.01; Figure 3). At GATA4, differences were more evident in the Cosnino flock (n_S = 48, n_{NS} = 310, X^2 = 6.912, p = 0.07; Figure 4).

Average rho was higher before (average rho = 0.02) and after the drought (average rho = 0.06) than it was during the drought (average rho = 0.00) (Figure 5).

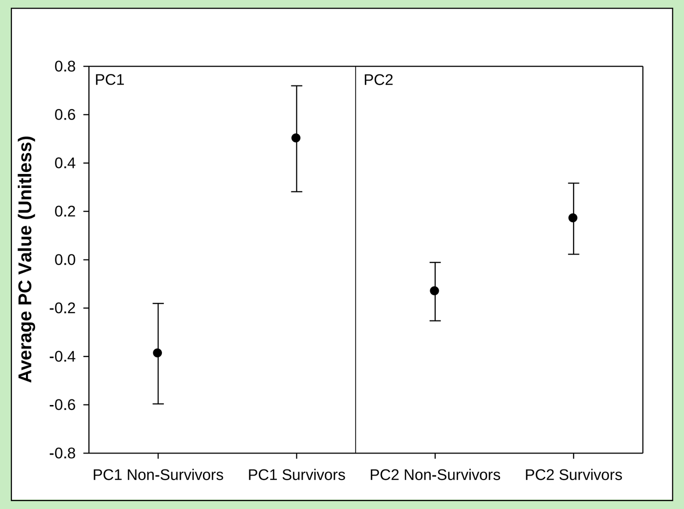


Figure 2. Differences in average PC1 (n_S = 106, n_{NS} = 141, t = 2.45, p = 0.01) and PC2 (n_S = 106, n_{NS} = 141, t = 1.75, p = 0.08) values for non-survivors and survivors. Error bars represent ±1 SEM.

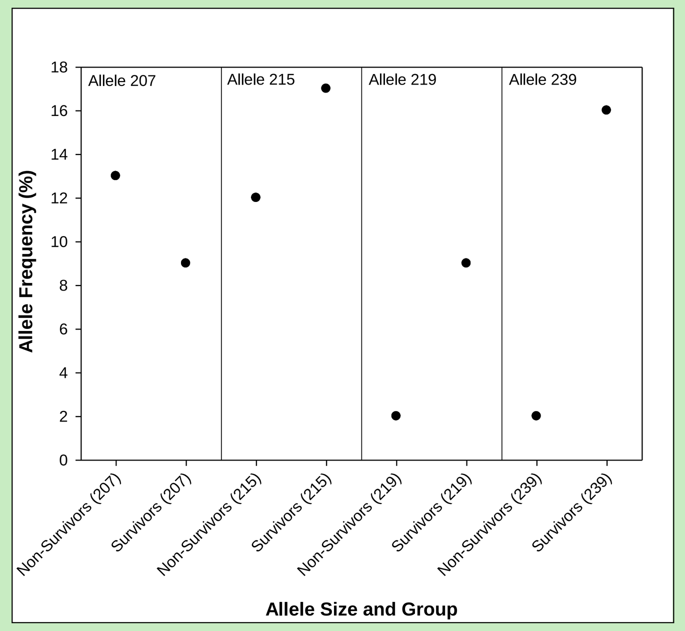


Figure 3. Frequencies of alleles 207, 215, 219 and 239 at AAAG9 for non-survivors and survivors.

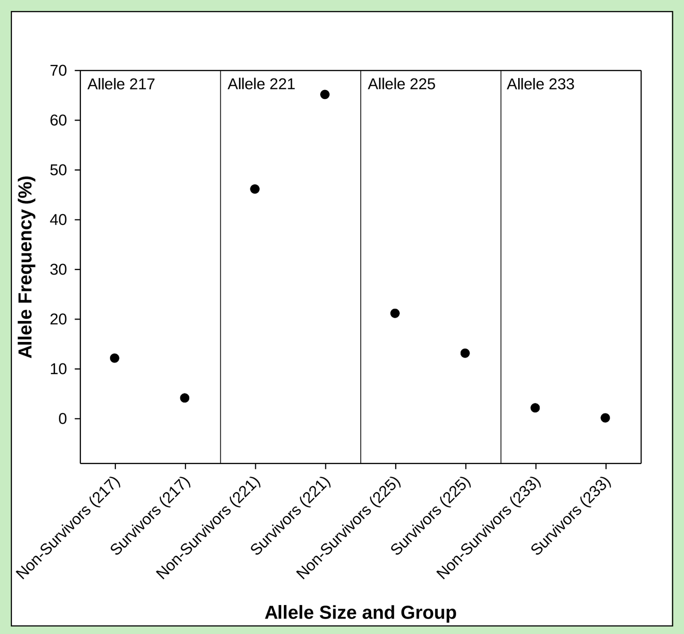


Figure 4. Frequencies of alleles 217, 221, 225 and 233 at GATA4 for non-survivors and survivors.

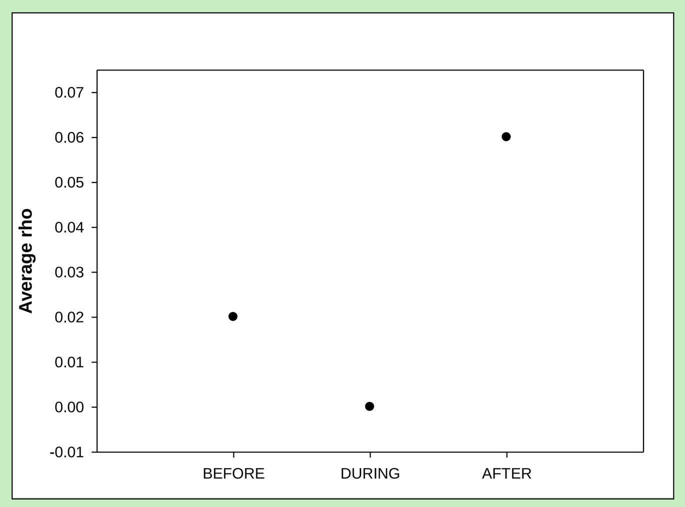


Figure 5. Average rho values before (0.02), during (0.00), and after (0.06) the drought.

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 higher social status survived differentially. Birds with greater physiological capacity might have had a greater ability to survive food shortages, temperature extremes, metabolic demands of producing offspring, 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).

Individuals with certain genotypes at two 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 into the long term effects of the 2002-03 drought and the resulting population bottleneck in keystone and ancillary species is necessary.

References

Balda, R.P. 2002. Pinyon Jay (Gymnorhinus cyanocephalus). In A. Poole & F. Gills (Eds.), *The Birds of North America* (No. 605) Philadelphia: The Birds of North America, Inc.

Benford, R., Menses, N., Service, P.M., and Balda, R.P. 2006. Potential causes of unexpected structure in a metapopulation of pinyon jays. 24th International Ornithological Congress. Hamburg, Germany.

Boag, P.T. and Grant, P.R. 1981. Intense natural selection in a population of Darwin's Finches (Geospizinae) in the Galápagos. *Science* 214: 82-85.

Brown, J.H., Whitham, T.G., Ernest, S.K.M., Gehring, C.A. 2001. Complex species interactions and the dynamics of ecological systems: Long-term experiments. *Science* 293: 643-650.

Bumpus, H.C. 1899. *The elimination of the unfit as illustrated by the introduced House Sparrow,* Passer domesticus. Biological Lectures, Marine Biology Laboratory, Woods Hole: 209-226.

Busch, J.D., Benford, R., Pearson, T., Palmer, E., Balda, R.P., and Keim, P. Submitted. New polymorphic tetranucleotide repeats for pinyon jays (*Gymnorhinus cyanocephalus*). *Molecular Ecology Notes*.

Gitlin, A.R., Sthultz, C.M., Bowker, M.A., Stumpf, S., Paxton, K.L., Kennedy, K., Muñoz, A., Bailey, J.K., Whitham, T.G. 2006. Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conservation Biology* 20: 1477-1486.

Goodman, S.J. 1997. RST CALC: A collection of computer programs for calculating unbiased estimates of genetic differentiation and determining their significance for microsatellite data. *Molecular Ecology* 6: 881-885.

Harter, L.B., Benford, R., Balda, R.P. 2006. *Is seed handling behavior optimized for social status in pinyon jays* (Gymnorhinus cyanocephalus)*?* Poster presented at the 4th North American ornithological Conference, Veracruz, Mexico.

IPCC (Intergovernmental Panel on Climate Change). 2001. *Climate Change 2001: the Scientific Basis.* Cambridge University Press, Cambridge.

Marzluff, J.M. and Balda, R.P. 1992. *The Pinyon Jay: Behavioral Ecology of a Colonial and Cooperative Corvid.* T & AD Poyser, London.

National Oceanic and Atmospheric Administration. 2008. http://www.noaa.gov. Accessed March 23, 2008.

Strasser, E.H., Benford, R., Balda, R.P. 2006. *Linear hierarchy provides context for evolution of social cognition in pinyon jays.* Poster presented at the 4th North American ornithological Conference, Veracruz, Mexico.

Wiggins, D.A. 2005. *Pinyon Jay* (Gymnorhinus cyanocephalus)*: A Technical Conservation Assessment.* Prepared for USDA Forest Service.

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