

## BRIEF REPORT

# Fourteen Tail Feathers: An Autosomal Recessive Trait in California Condors (*Gymnogyps californianus*)

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Eight pairs of California Condors (*Gymnogyps californianus*) have produced 12 chicks with 14 tail feathers instead of the normal 12. The 14 tail feather trait appears to follow an autosomal recessive pattern of inheritance and is not known to be deleterious. The putative allele for the trait was present in at least seven of the 13 founders of the population. The 14 tail feather allele is the second recessive allele discovered in the condor population. Due to the founder effect, which changes the frequency of many formerly rare recessive alleles, and genetic management to minimize mean kinship, which reduces the expression of recessive traits, it is likely that this population carries other recessive alleles that have not yet been detected. Zoo Biol. XX:XX–XX, 2016. © 2016 Wiley Periodicals, Inc.

**Keywords:** tail feather; founder effect; recessive alleles; California Condors; *Gymnogyps californianus*

## INTRODUCTION

California Condors (*Gymnogyps californianus*) underwent a precipitous population decline after European colonization of North America; however, a small wild population persisted in California until the 1980s [Snyder and Snyder, 2000; Ralls and Ballou, 2004]. High mortality continued and the last three wild condors were brought into captivity in 1987 [Wallace and Toone, 1992; Snyder and Snyder, 2000]. Condors bred well in captivity and the first releases of captive-reared individuals occurred in 1992 in Southern California. As of December 31, 2015 the population consisted of 435 individuals: 167 in captivity and 268 wild birds divided among three reintroduced populations in California, Arizona/Utah, and Baja California, Mexico [USFWS, 2016].

The California Condor population is managed to minimize mean kinship [Ralls and Ballou, 2004], which reduces the expression of recessive alleles because matings between close relatives are avoided. In the captive part of the population, new pairs are established to minimize mean kinship; in the wild populations, individuals choose their own mates and kinship is minimized as much as possible by the annual addition of genetically appropriate individuals.

Some recessive alleles are likely present at relatively high frequencies in the population due to a founder effect.

When populations become small, many rare recessive alleles are lost but a few, by chance, increase in frequency. Instances in which a recessive allele that was rare in the general population became common in a small subpopulation are well known in humans [Diamond and Rotter, 1987]. Deleterious recessive alleles have been described in several captive populations that were founded by a small number of individuals [Laikre, 1999; Frankham et al., 2010].

A deleterious recessive allele for chondrodystrophy, a lethal form of dwarfism, occurs at relatively high frequency in the California Condor population [Ralls et al., 2000]. Here we report on a second recessive trait in the California Condor

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## 2 Pryor and Ralls

population: 14 tail feathers. Condors normally have 12 tail feathers.

### MATERIALS AND METHODS

U. S. Fish and Wildlife Service (USFWS) staff routinely capture wild condors in Southern California for management purposes that include attaching at least one very high frequency (VHF) radio-transmitter to a central tail feather [Hall et al., 2007; USFWS, 2014], checking which tail feather is most suitable for a transmitter and recording any missing, growing, or broken tail feathers. During a handling event in July 2011, USFWS staff noticed that studbook number 247 had 14 tail feathers. In October 2012, they observed 14 tail feathers on studbook number 137, condor 247's full sibling, while he was being prepared for release after being transferred from the Oregon Zoo. The discovery of a second California Condor with 14 tail feathers prompted us to obtain data on the number of tail feathers in as many condors as possible.

We asked staff of the organizations that manage captive or wild condors to count the number of tail feathers in living birds that were being handled for health exams, transfer, or other purposes and dead birds in freezers or being necropsied. The data set we obtained is provided as electronic supplementary material. We drew the pedigree of the individuals with 14 tail feathers back to the founders of the population based on parentage data recorded in the California Condor studbook [Mace, 2016]. The complete pedigree of the population, including both wild and captive individuals, is known because genetic samples are taken from chicks and parentage of both wild and captive chicks is routinely confirmed or determined by microsatellite genotyping in the genetics laboratory at the San Diego Zoo Institute for Conservation Research.

We assumed that tail feather phenotype did not affect the probability that a bird's phenotype was known and thus that our sample of birds with known phenotypes was a random sample. We compared the ratio of affected (14 tail feathers) to normal birds (12 tail feathers) among the offspring of the pairs in which both parents had or could have had the normal phenotype to that expected if the allele for 14 tail feathers was an autosomal recessive (one affected to three unaffected) with a chi-square Goodness of Fit test. We compared the sex ratio of the affected chicks to that of the unaffected chicks with Fisher's Exact Test. Both tests were done with the online calculators at VasserStats [Lowry, 1998–2016].

### RESULTS

Utilizing a partial pedigree of the California Condor population (Fig. 1), we identified eight condor pairs that produced at least one individual with 14 tail feathers. The putative allele for 14 tail feathers cannot be dominant, as four pairs in which both birds have normal phenotypes ( $20 \times 13$ ,  $20 \times 29$ ,  $33 \times 13$ , and  $125 \times 111$ ) have produced affected

individuals. If the allele was sex-linked, the majority of affected individuals should be females (females are the heterogametic sex in birds). However, there are both male and female birds with 14 tail feathers (Fig. 1). In the eight sibships containing an affected bird, the sex ratio of the birds known to be affected (2 females:10 males) was not significantly different than the sex ratio of the birds known to be unaffected (12 females:14 males) (Fisher's Exact Test Statistic = 0.1470, d.f. = 1,  $P = 0.1470$ ). The allele appears to exhibit autosomal recessive inheritance. Excluding the one sibship in which one parent was affected, there were seven sibships in which both parents were known to have or might have had normal phenotypes. In these sibships, the relative numbers of known affected and unaffected birds (12 and 26, respectively) were not significantly different from those expected under autosomal recessive inheritance (one affected to three unaffected) ( $\chi^2 = 0.56$ , d.f. = 1,  $P = 0.4543$ ). At least seven founders must have carried at least one copy of the putative allele for 14 tail feathers: 1, 6, 7, 12, and 13, and either 2 and/or 11 and 4 and/or 8 (Fig. 1). Unlike the autosomal recessive allele for chondrodystrophy in the California Condor population [Ralls et al., 2000], the 14 tail feather allele does not appear to be severely deleterious.

### DISCUSSION

We document the presence of an autosomal recessive allele for 14 tail feathers in the California Condor population. No cases of extra tailfeathers in wild bird species are known [Bartels, 2003]. Extra tail feathers are known in domestic pigeons (*Columba livia*) and chickens (*Gallus gallus*). Darwin [1868] described variation in the number of tail feathers in pigeons. Morgan [1918] and Johansson [1927] attempted to determine the genetic basis of extra tail feathers in Fantail pigeons but the pattern of inheritance appeared to be rather complicated, involving at least 3–4 loci. Williams [1979] reported that some bantam chickens have eight rather than six tail feathers. Eight tail feathers is a trait with single locus autosomal recessive inheritance but incomplete penetrance and variable expressivity. Somes [1990] also lists eight tail feathers as a single-locus trait in chickens. The 14 tail feather trait in condors appears to resemble the bantam case more closely than the pigeon case, although it is not necessarily due to a mutation in the same gene. No deleterious effects of the allele have been noted but it could, for example, be mildly deleterious in the wild but not in captivity.

The putative allele for 14 tail feathers must have been fairly common in the wild population immediately prior to the capture of all remaining condors in 1987 [Wallace and Toone, 1992; Snyder and Snyder, 2000]. Genetic management to minimize mean kinship in the population reduces the expression of recessive alleles and increases the likelihood that such alleles will remain undetected. Due to the founder effect and genetic management to minimize mean kinship, it is likely that the California Condor population carries other recessive alleles that have not yet been detected.

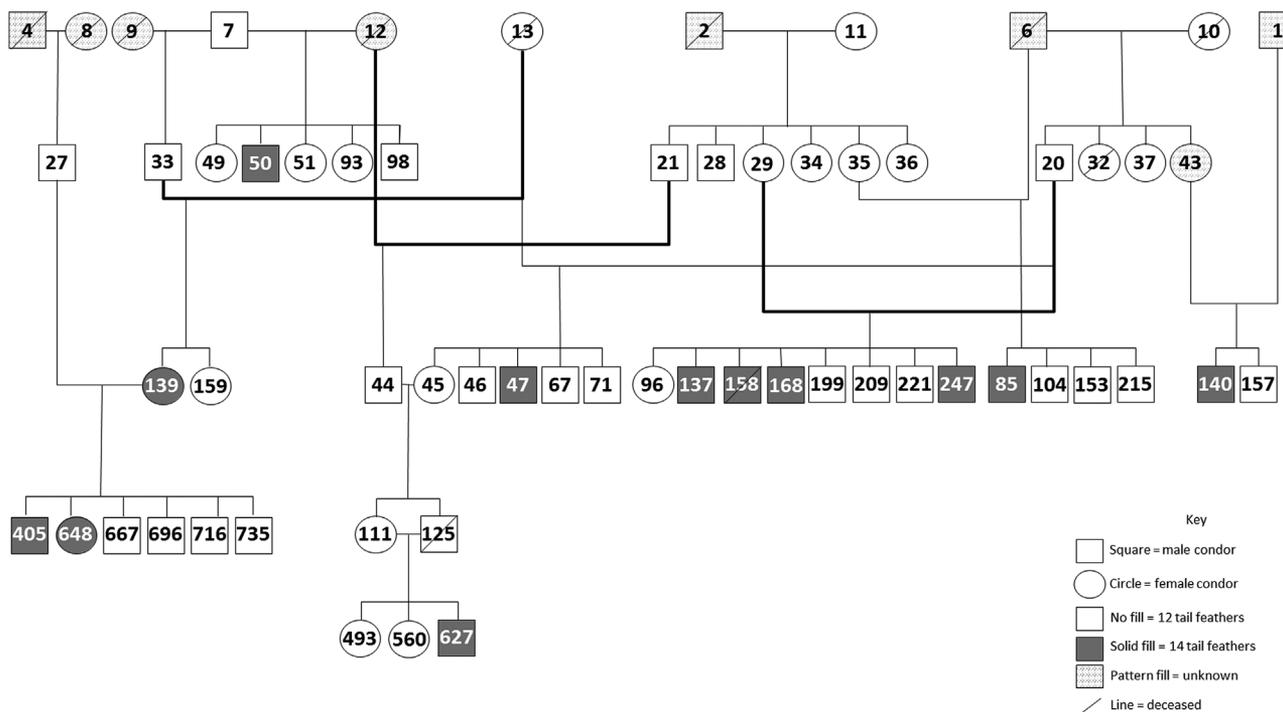


Fig. 1. Partial pedigree of the California Condor population, showing relationships of the birds with 14 tail feathers. Individuals are identified by their studbook numbers. The 11 founders contributing to this part of the pedigree are shown in the top row. Studbook number 20 was thought to be a founder [Ralls and Ballou, 2004] until whole-genome sequencing revealed that he was the son of founders 6 and 10 [Ryder et al., 2014]. Siblings of birds with 14 tail feathers that have an unknown number of tail feathers are not shown in the pedigree but are included in the electronic supplementary material.

**CONCLUSIONS**

- Eight pairs of California Condors have produced 12 chicks with 14 instead of the normal 12 tail feathers.
- The 14 tail feather trait appears to follow an autosomal recessive patterns of inheritance.
- No deleterious effects of the allele have been noted to date.
- The allele for the trait was present in at least seven of the 13 founders of the population: 1, 6, 7, 12, and 13, and either 2 and/or 11 and 4 and/or 8.
- Due to the founder effect and genetic management to minimize mean kinship, it is likely that the California Condor population carries other recessive alleles that have not yet been detected.

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#### 4 Pryor and Ralls

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#### SUPPORTING INFORMATION

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