

Original Article

Facultative Parthenogenesis in California Condors

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Abstract

Parthenogenesis is a relatively rare event in birds, documented in unfertilized eggs from columbid, galliform, and passerine females with no access to males. In the critically endangered California condor, parentage analysis conducted utilizing polymorphic microsatellite loci has identified two instances of parthenogenetic development from the eggs of two females in the captive breeding program, each continuously housed with a reproductively capable male with whom they had produced offspring. Paternal genetic contribution to the two chicks was excluded. Both parthenotes possessed the expected male ZZ sex chromosomes and were homozygous for all evaluated markers inherited from their dams. These findings represent the first molecular marker-based identification of facultative parthenogenesis in an avian species, notably of females in regular contact with fertile males, and add to the phylogenetic breadth of vertebrate taxa documented to have reproduced via asexual reproduction.

Subject Area: Conservation genetics and biodiversity, Molecular systematics and phylogenetics

Keywords: California condor, conservation genetics, parthenogenesis

Bi-parental inheritance is a hallmark of vertebrate reproduction, although the list of exceptions is growing (Watts et al. 2006; Lampert 2008; Neaves and Baumann 2011; Booth et al. 2012; Fields et al.

2015). Obligate parthenogenesis has evolved in multiple species as the mode of reproduction, in which development occurs exclusively without male contribution. Facultative parthenogenesis is a

form of asexual reproduction in females that typically reproduce sexually. Both forms of parthenogenesis involve meiotic segregation, but reconstitution of diploidy may differ. In mammals, the imprinting of genes involved in placentation, resulting in their expression from the paternal genome (see [Peters 2014](#) for a review), seemingly precludes parthenogenetic reproduction in eutherians in which females are the homogametic sex. Parthenogenetic development is recognized to occur in some reptilian species, under situations where females have been isolated without mates, but also occurs in natural populations of reptiles and fishes ([Booth et al. 2012](#); [Fields et al. 2015](#)).

In birds, observation of parthenogenesis has been confined mainly to domestic turkeys and chickens separated from males. The work of M.W. Olsen and colleagues identified parthenogenetic development in turkeys that produced fertile parthenote males ([Olsen 1965](#); [Olsen et al. 1968](#)). Additionally, initiation of parthenogenetic development that failed to progress to hatching was noted in a study group of captive female finches ([Schut et al. 2008](#)) and in the domestic pigeon ([Bartelmez and Riddle 1924](#)). Here, we report molecular genetic evidence for parthenogenetic development of two California condors (*Gymnogyps californianus*), a species of New World vulture in the Order Cathartiformes. The two individuals were produced by two different females, each of which was housed with a fertile male as part of the captive breeding program for species recovery.

From a low of 22 birds in 1982 ([USFWS 1996](#)), the critically endangered California condor population has steadily increased through captive breeding and reintroduction of birds into the wild. As the population of California condors was expanded, breeding recommendations incorporated molecular-based estimations of relatedness of the founder birds ([Geyer et al. 1993](#)), avoided mating known relatives, and retained genetic variation through mating individuals with low mean kinship ([Ralls and Ballou 2004](#)). More than 1,000 chicks have been produced since the program began in 1988. By the end of 2019, the extant population consisted of 525 birds, 219 in captivity and 306 wild individuals free-flying in California, Arizona, Utah (including the Grand Canyon area and Zion National Park), and Baja California ([Mace 2019](#)). The successful restoration program also benefited from genetic and genomic research projects in this endangered species ([Romanov et al. 2006](#); [Modi et al. 2009](#)). A California condor microsatellite-enriched library and a set of polymorphic microsatellite markers were generated and used as an instrument for genetic studies ([Romanov et al. 2009](#)). More recently, a comprehensive evaluation and refinement of microsatellite variation in the entire pedigree was reported ([Moran et al. 2021](#)). This case-by-case parentage qualification utilizing 21 California condor-derived microsatellites was initiated for chicks produced in the wild population to corroborate behavioral observations and ensure the accuracy of the California Condor International Studbook ([Mace, 2019](#)).

In the case of the California condor parthenotes, exclusively maternal genetic contributions for two offspring were discovered through analysis of condor-derived DNA microsatellites as part of the comprehensive genotype survey. These two birds were the only condors homozygous at all assayed loci. Additionally, both chicks had been identified as males by genetic sexing methods, which is expected under facultative parthenogenesis. These data support facultative parthenogenesis as the mechanism that produced the homozygous genotypes of both male condors. Although only documented to date in the captive population, these findings have potential demographic implications that recommend continued

genotyping efforts in the future, as well as revealing another avian order in which parthenogenesis has been identified.

Materials and Methods

Samples

California condor samples from the 911 individuals in this study were collected opportunistically over the course of the program's 30+ year history and include blood, eggshell membrane, tissue from deceased birds, and feathers collected according to USFWS and IACUC approval. DNA was isolated using either a modified phenol-chloroform extraction method ([Sambrook et al. 1989](#)) or via a column-based method using the QIAamp DNA Mini Kit (Qiagen Inc.) following the manufacturer's protocol. DNA samples were stored at 4 °C until their use in polymerase chain reactions (PCR).

Microsatellite Analysis

Microsatellite genotyping was performed using 21 polymorphic loci as described in [Moran et al. 2021](#). Strategies were used to identify genotyping errors: 1) California Condors were genotyped multiple times, 2) statistical tests were conducted to reveal deviation from Hardy–Weinberg equilibrium and homozygous excess resulting from either null alleles or allelic dropout; and 3) visual inspection of trios by comparing assigned parents with offspring genotypes ([Moran et al. 2021](#)).

The generation of the homozygous genotypes consisting of only one maternal allele—indicative of parthenogenesis—was identified by eye after discovering two birds that did not qualify to their presumed sire and were excluded at multiple loci. The likelihood of uniparental inheritance of presumable parthenogenetic condors was estimated in Cervus 3.0 ([Kalinowski et al. 2007](#)) by performing parentage analysis using the microsatellite genotypic data. For each parthenote bird, the paternity analysis calculates likelihood ratio (LOD) scores for candidate pairs and trios, and the Delta score that represents the difference in LOD scores between the first and second most likely candidate parents. Parentage assignment was determined by including the genotypes of the known dams (SB35 and SB39), all California condor males genotyped since the establishment of the breeding program, and genotypes of hypothetical candidate sires that were identical to each of the respective dam's genotypes for determining uniparental inheritance. Parentage was assigned with 95% confidence. All parentage assignments were validated by visual screening of genotypes and based on metadata of captive and wild condors that include location and age of candidate parents at time of hatch date of offspring.

Results

The effort to generate microsatellite genotypes for all California condors identified two birds, studbook number SB260 (who died at 1.9 years of age) and SB517 (who died at 7.9 years of age), whose microsatellite profiles revealed that they qualified as the offspring of their studbook dams, but were excluded from their assigned sires at unexpectedly high numbers of loci (8 and 6 loci, respectively; [Table 1](#)). SB260 and SB517 were sexed as males using a test for sex-chromosome specific genetic markers ([Kahn et al. 1998](#)) and genotyped on multiple occasions, five and three times, respectively. Upon further inspection, both birds were found to be homozygous for their respective dam's alleles at all 21 microsatellite markers ([Supplementary Table 1](#)). The two chicks identified as parthenotes

Table 1. The informative microsatellite (msat) loci used in determining parthenogenesis of studbook numbers 260 and 517

	“sire”	dam	parthenote	“sire”	dam	parthenote
	SB6	SB35	SB260	SB42	SB39	SB517
msat loci						
109D	194/218	194/222	194/194	194/218	194/222	222/222
125G	187/187	181/187	181/181	179/187	187/187	187/187
133H	235/239	235/239	235/235	219/235	231/235	231/231
144A	207/221	207/209	209/209	209/221	207/221	207/207
151F	151/163	151/160	160/160	151/169	157/160	157/157
A8	227/229	215/227	215/215	229/229	213/227	227/227
C5	180/186	180/192	180/180	180/180	192/192	192/192
D24	166/166	170/170	170/170	166/170	166/170	170/170
H3	121/121	121/129	129/129	121/121	121/129	121/121
H6	123/123	115/123	115/115	115/123	115/123	123/123
H106	241/241	217/241	217/217	217/241	241/241	241/241

The presumptive sire for 260 (SB6) is excluded at eight msat loci, and studbook sire of 517 (SB42) is excluded at six msat loci; the exclusionary alleles are bolded. SB35 qualifies as dam of 260 and SB39 qualifies as dam of 517 for all loci studied (see [Supplementary Table 1](#)).

Table 2. Parentage analysis parameters of parthenogenetic California condors SB260 and SB517

Parthenogenetic offspring ID	260	517
Known dam ID	35	39
Loci typed	21	21
Dam loci compared	21	21
Dam loci mismatching	0	0
Dam LOD score	8.92	7.13
Dam Delta	8.92	7.13
Dam confidence	*	*
Candidate sire ID	35a	39a
Loci typed	21	21
Sire loci compared	21	21
Sire loci mismatching	0	0
Sire LOD score	8.92	7.13
Sire Delta	4.09	3.86
Sire confidence	*	*
Trio loci compared	21	21
Trio loci mismatching	0	0
Trio LOD score	17.9	14.3
Trio Delta	4.43	4.09
Trio confidence	*	*

Known dams are SB35 and SB39, respectively, and sire genotypes identical to the known dam genotypes are represented by SB35a and SB39a. Asterisks indicate significant Delta scores.

were the only individuals from among 911 condors in our genotype database that were homozygous at all examined loci.

Among 467 male California condors tested in the parentage analysis, no male qualified as a potential sire of the two presumptive parthenote birds. When uniparental inheritance was tested by including candidate sire genotypes that were identical to the known dam genotypes, we obtained positive and significant LOD and Delta scores for the pair and trio ([Table 2](#)) that support the condors SB260 and SB517 as being produced by parthenogenesis.

Discussion

Avian parthenogenesis has been observed previously, and in most instances results in arrested development ([Schut et al. 2008](#); [Parker](#)

[et al. 2014](#)). Perhaps the earliest report of parthenogenetic initiation of development was in a columbid, the domestic pigeon ([Bartlemez and Riddle 1924](#)). Galliform species, including domestic chickens and Chinese painted quail raised in the absence of males, have produced eggs reported to infrequently initiate embryogenesis and extremely rarely produce a viable male chick ([Sarvella 1973](#); [Parker and McDaniel 2009](#)). Among Passeriformes, zebra finch eggs produced under conditions without males were noted to initiate early stages of development, but embryogenesis was always arrested ([Schut et al. 2008](#)). Live chicks, and more rarely fertile adults, resulting from parthenogenetic developments have been observed, notably in domestic turkeys, in which viable chicks developed from unfertilized eggs where males were not present ([Olsen 1965](#)).

Unlike the other examples of avian parthenogenesis, the absence of a suitable male does not explain the two occurrences of parthenogenetic development in California condors that we have identified. We believe that our findings represent the first example of facultative avian parthenogenesis that does not involve segregation of the sexes. The dams of both birds had each been continually housed for a number of years with a single male with which they had reproduced sexually. The dam of SB260 had 11 chicks via sexual reproduction with the same male before laying the egg that produced her parthenote offspring. The dam of SB517 was paired with a male California condor for 20 years and produced 23 chicks for which bi-parental inheritance can be demonstrated prior to her parthenote offspring. She has since reproduced sexually twice more with her mate.

These findings are consistent with automixis, involving gametic fusion or endomitosis, as the mechanism of oocyte production ([Lampert 2008](#)). Additional markers could clarify whether automixis with terminal fusion or endomitosis after meiosis, involving the duplication of a haploid genome, resulted in partially or completely homozygous offspring, respectively. [Card et al. \(2021\)](#) provided evidence for terminal automixis fusion in the king cobra utilizing genome-wide data from reduced representation sequencing. The use of the recently published chromosome-level reference genome of the California condor ([Robinson et al. 2021](#)) and genome re-sequencing efforts can map genetic variation genome-wide to evaluate the mechanism of parthenogenesis in this species.

The ability of a female condor to produce a male offspring via parthenogenesis has potential demographic and genetic implications.

For example, this form of reproduction could assist range expansion when populations are at very low densities (Lampert 2008). The tendency to reproduce parthenogenetically also has implications for the extent of genetic variation in the species as a whole, depending on the frequency of parthenotes produced. Likely due to the severe population bottleneck they experienced, California condors exhibit very low microsatellite diversity. The set of 21 microsatellite loci utilized in parentage and population analyses has a mean of 3.1 alleles per locus (Moran et al. 2021) and these were drawn from the most polymorphic candidate loci, with many apparently monomorphic loci detected. The occurrence of a recessive lethal allele resulting in a lethal form of dwarfism, known as chondrodystrophy, in California condors (Ralls et al. 2000) is consistent with inbreeding in a small population. Neither dam that produced the parthenogenetically developed chicks ever produced a chondrodystrophic chick, but to date, carriers for the chondrodystrophy mutation can only be identified if they produce an affected chick. It is self-evident that no recessive lethal alleles were inherited from the dam in either parthenote condor because they would not have survived. Sub-lethal impacts of parthenogenesis may reduce fitness while, simultaneously, lethal genetic load is reduced (Hedrick 2007).

Both parthenote California condors are now deceased. SB260 was released into the wild at 559 days of age and died at 718 days (1.96 years) of age, prior to sexual maturity. Death was attributed to poor body condition due to poor integration with the wild birds and insufficient food consumption. SB517 was never released into the wild and died at 2915 days (7.98 years) of age. He was a small bird; as an adult, his weight varied from 6.1 to 6.8 kg, whereas the average weight for adult condors is considered to be 8–10 kg (Walker K, personal communication). He shared an enclosure with a female, but was considered submissive with limited or no courtship behavior. For this bird, death was attributed to systemic complications following injury to a foot and digit amputation. The bird also had scoliosis, which had been noted prior to death, and probably explained an abnormal gait when walking. Other studies of parthenogenetic reproduction in snakes have also noted deformities in parthenogens (Booth and Schuett 2016; Card et al. 2021). Neither of these birds had reproduced, and none of the post-mortem findings could conclusively be considered to be indicators of lack of fitness. Therefore, unless additional cases are identified, determination of reproductive capability of California condor parthenotes will be precluded.

California condors experienced a population bottleneck with all genetic diversity descending from 14 birds, some of which were related (Geyer et al. 1993). Utilizing estimation of relatedness of founders based on molecular analysis, the overall inbreeding coefficient of the current California condor population is $F = 0.0169 \pm 0.04909$ std. dev., as matings have been managed through pairing birds of low mean kinship (Ralls et al. 2000). The coefficient of inbreeding of the parthenotes is $F = 1$, if all of their loci are identical-by-descent from their dam.

Facultative parthenogenesis in vertebrates has generally been considered limited and phylogenetically restricted, although now repeatedly noted in avian, reptilian (Booth and Schuett 2016; Card et al. 2021), and elasmobranch taxa (Fields et al., 2015). It has been hypothesized that populations at low density may be more likely to have individuals reproduce parthenogenetically (Fields et al. 2015). Facultative parthenogenetic reproduction, when the majority of population recruitment is due to sexual reproduction, may contribute to reducing genetic load via purging of deleterious mutation (Hedrick 2007). Additionally, a condor female that mates

with a parthenote male would not be expected to produce chicks homozygous for a lethal trait. The potential impact of concomitant purging of deleterious mutations and increase in inbreeding through parthenogenesis may need to be more broadly examined as more instances of facultative parthenogenesis are described.

We believe that this is the first study to use molecular markers to identify facultative parthenogenesis in an avian species. This novel finding in California condor females housed with fertile males raises the question of unrecognized parthenogenesis in other avian species (Fields et al. 2015). Detection of parthenogenesis is generally difficult, and typically discoveries have been aided by observing reproduction under circumstances in which the female has not had an opportunity to mate. However, with the California condors, both dams produced sexually numerous times and continued to be housed with fertile males, as was noted for parthenogenesis in some non-avian species (Booth et al. 2011, 2014). Recently, a generalized method for identifying parthenotes in wild populations by evaluating internal relatedness of individuals in a population has been developed (Fields et al. 2015). However, the genetic basis for induction of parthenogenesis in vertebrates remains elusive and the impacts on genetic variation and evolutionary potential will depend on the frequency of production of parthenotes (Fields et al. 2015). In species of fowl, the frequency of unfertilized eggs initiating parthenogenetic development has been shown to be a selectable trait (Olsen 1965; Parker et al. 2010).

Vertebrate species in which individuals are able to produce viable offspring using both sexual and parthenogenetic modes of reproduction in captive and wild populations occurs widely across major vertebrate groups including reptiles, birds, bony fish, and six species of sharks and rays (Olsen 1965; Watts et al. 2006; Chapman et al. 2007, 2008; Lampert 2008; Feldheim et al. 2010; Booth et al. 2011a; Booth et al. 2011b; Neves and Baumann 2011; Robinson et al. 2011; Booth et al. 2012; Reynolds et al. 2012; Booth et al. 2014; Fields et al. 2015; Booth and Schuett 2016; Harmon et al. 2016). For wild populations of reptiles, parthenogenetic reproduction was identified by unexpected homozygosity across multiple loci (Booth et al. 2012). Recently parthenogenetic reproduction has been identified in wild populations of an elasmobranch fish, the smalltooth sawfish, by evaluating relatedness of individuals within a population (Fields et al. 2015). While our study was not designed to test for parthenogenetic reproduction, the number of condors analyzed, the number of loci utilized, and the access to DNA from practically every individual of the species since its precipitous decline in 1986–1987 contributed to the power of our analysis and effectively excluded other possible explanations. The propensity for parthenogenetic development in avian phylogeny is becoming better known, with examples occurring in three avian orders: Galliformes, a basal clade, Passeriformes, Columbiformes, and, as shown here, Cathartiformes.

Facultative parthenogenesis in the California condor breeding program accounts for approximately 2.4% of all reproducing female condors evaluated here, similar to the estimated frequency in pit viper snake populations (Booth et al. 2012). Finding two cases of parthenogenesis in the studied population of birds, which at the time comprised 99% of all captive condor reproduction and 89% of the entire wild and captive condor reproduction occurring since breeding management was initiated, suggests that parthenogenesis in California condors may be a recurrent phenomenon and constitutes a portion of the species' overall reproductive effort. As reproduction in reintroduced California condors is behaviorally more

complex than under human management, involving interaction with multiple conspecifics of both sexes, ongoing genetic monitoring of the increasing number of wild-bred condor chicks will help determine whether facultative parthenogenesis in California condors is limited to the managed breeding program. Furthermore, genetic monitoring and management of California condor recovery will benefit from accurate parentage identification, whether biparental or uniparental.

Genetic analysis of museum specimens could also shed light on this question and assist in understanding the evolution of facultative parthenogenesis, its genetic basis, and contribute to comprehending the levels of genetic variation in the recovering California condor population. Additionally, the use of the high-quality reference genome for the California condor (Robinson et al. 2021) and generation of genomic sequence data at the population level will allow validating the parthenogenetic observations made based on microsatellite data.

Supplementary Material

Supplementary data are available at *Journal of Heredity* online. [Supplementary Table 1](#). Genotyping at 21 microsatellite loci for parthenotes, their dams, and co-housed males that were putative sires. Data from Moran et al. (2021).

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Data Availability

We have deposited the primary data underlying these analyses as follows: [Moran et al. \(2021\)](#).

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