FEATURE ARTICLES

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GENETIC STATUS AND MANAGEMENT OF CALIFORNIA CONDORS

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Abstract. The last wild California Condor (*Gymnogyps californianus*) was brought into captivity in 1987. Captive breeding was successful and reintroduction efforts began in 1992. The current population is descended from 14 individuals belonging to three genetic ''clans.'' This population bottleneck led to the loss of genetic variation and changes in allele frequencies, including a probable increase in the frequency of the putative allele for chondrodystrophy, a lethal form of dwarfism. We use studbook data to analyze the current genetic and demographic status of the population and explain how it is managed to meet specific goals. In August 2002 the population consisted of 206 individuals distributed among three captive-breeding facilities and three reintroduction sites. The population is managed to preserve genetic diversity using the concept of mean kinship. Growth of the total population has been between 10% and 15% per year since 1987, but the growth of the captive population has been only about 5% per year since 1992 due to the removal of chicks for reintroduction. Assuming that founding birds within clans were half-siblings, the birds used to found the captive population theoretically contained 92% of the heterozygosity present in the hypothetical wild base population. About 99.5% of this heterozygosity has been retained in the current population. Alleles from most founders are well represented across captive-breeding facilities and reintroduction sites. The genetic status of this population compares favorably with other species that have been rescued from extinction by captive breeding.

Key words: California Condor, captive breeding, genetic management, Gymnogyps californianus, *reintroduction.*

Situación Genética y Manejo de *Gymnogyps californianus*

Resumen. El último cóndor californiano (*Gymnogyps californianus*) silvestre fue puesto en cautiverio en 1987. La reproducción en cautiverio fue exitosa y las reintroducciones comenzaron en 1992. La población actual desciende de 14 individuos pertenecientes a tres ''clanes'' genéticos. Este cuello de botella poblacional dió lugar a la pérdida de variabilidad genética y a cambios en la frecuencia de alelos, incluyendo un probable incremento en la frecuencia del alelo para condrodistrofia, una forma letal de enanismo. En este estudio, utilizamos datos del libro genealógico para analizar la situación genética y demográfica actual de la población y para explicar cómo se está manejando la población para cumplir con metas específicas. En agosto del 2002 la población consistía de 206 individuos distribuidos en tres instalaciones de reproducción en cautiverio y tres sitios de reintroducción. La población fue manejada con el propósito de conservar la diversidad genética usando el concepto de parentesco medio. El crecimiento de la población ha sido de entre 10% y 15% por año desde 1987, pero el crecimiento de la población en cautiverio ha sido únicamente de aproximadamente un 5% por año desde 1992 debido a la remoción de los pollos para su reintroducción. Suponiendo que los cóndores fundadores dentro de cada clan eran medio-hermanos, las aves que fueron utilizadas para fundar la población en cautiverio teóricamente

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contienen un 92% de la heterocigosidad presente en la población silvestre base hipotética. Cerca de un 99.5% de esta heterocigosidad ha sido retenida en la población actual. Alelos de la mayoría de los fundadores están bien representados en las diversas instalaciones de reproducción en cautiverio y sitios de reintroducción. La situación de esta población parece ser mejor que la de otras especies silvestres que han sido rescatadas por medio de la reproducción en cautiverio.

INTRODUCTION

California Condors (*Gymnogyps californianus*) once ranged over much of southern North America. After the end of the Pleistocene, the range of the species contracted toward the West Coast (Emslie 1987). After Europeans arrived, the population began a precipitous decline due to a variety of human impacts (Snyder and Snyder 2000). A small wild population persisted in California until the 1980s. However, high mortality continued and the last wild California Condor was brought into captivity in 1987 to avoid extinction of the species. The total population then consisted of 27 captive birds (Wallace and Toone 1992). Reproduction in captivity was highly successful and by August 2002 the population consisted of 206 individuals divided into four subpopulations: the captive population and reintroduced populations in California, Arizona, and Mexico.

Because of this population's history, pedigrees are available for every individual, regardless of its location. Thus, California Condors are one of the few species where management recommendations for both captive and wild populations can be based on pedigree analyses (Haig and Ballou 2002). Pedigree analyses provide powerful methods for describing current population structure, determining the genetic importance of specific individuals to current and future populations, and monitoring loss of genetic diversity over time (Haig and Ballou 2002). While pedigree analyses are routinely used for management of captive populations, they are unfortunately often unavailable for wild populations.

The California Condor population belongs to one of over 100 Species Survival Plans sponsored by the American Zoo and Aquarium Association (2003). These populations of threatened and endangered species are managed across the participating breeding facilities to retain, as far as possible, the genetic diversity present in the wild source population (Ralls and Ballou 1992, Frankham et al. 2002). Managing to maintain genetic diversity helps counter adaptation to the captive environment, minimizes possible deleterious effects of inbreeding, and preserves the population's capacity for genetic adaptation to environmental changes (Ralls and Ballou 1992).

Specific goals for the California Condor population include maximizing the growth of the captive population under the constraint of producing as many chicks as possible for reintroduction; ensuring that genetic diversity is well represented at each captive-breeding facility; minimizing the expression of chondrodystrophy (Thorp 1994), a lethal form of dwarfism (Ralls et al. 2002); transferring all the genetic diversity available in the captive population to the wild; and ensuring that each reintroduction site has the full genetic representation of the captive population. Decisions must be considered carefully, because it is often not possible to simultaneously maximize progress toward these multiple management goals.

Here, we use pedigree analyses to analyze the current demographic and genetic status of the condor population and illustrate how management decisions, such as choosing new pairs and deciding whether to reintroduce individual chicks to the wild, are made. Our specific objectives were to (1) determine the growth rate and age structure of the population; (2) determine the current genetic structure of the total population; (3) compare the genetic structure of the various subpopulations; and (4) conduct analyses to assist with 2002 management needs. These management needs included a genetic evaluation of existing pairs, recommendations for new pairings, identification of genetically less valuable birds that could be used for purposes other than breeding (e.g., as exhibit birds), selection of pairs to begin a new captive subpopulation at the Oregon Zoo, and recommendations for appropriate placement of the chicks hatched in 2002 in the various subpopulations.

METHODS

PEDIGREE ANALYSIS AND TERMINOLOGY

Pedigree analyses measure genetic parameters relative to a base population, which is assumed

to be a wild source population from which randomly captured individuals (founders) would be unrelated (i.e., the kinship coefficients among founders are 0.0; Falconer and Mackay 1996). Thus measures of genetic diversity determined by pedigree analyses estimate losses or changes relative to this hypothetical wild base or source population. Here we use the pedigree analysis software PM2000 (Pollak et al. 2002) to calculate changes in heterozygosity, levels of inbreeding, mean kinship among individuals, and survival and loss of founder alleles in the condor population.

Because of extensive work with domesticated, laboratory, and captive populations, software needed to carry out various pedigree calculations is widely available. Although some parameters such as inbreeding and kinship coefficients can be calculated directly (Ballou 1983), direct calculation of other parameters, such as survival probabilities for individual founder alleles, is beyond the capabilities of most desktop computers (Thompson 1983). Therefore, such probabilities are estimated with ''gene drop'' simulations (Mace 1986, MacCluer et al. 1986, Lacy 1989). Gene drop analyses begin by giving each founder two unique alleles. These unique alleles are then ''dropped'' down through the pedigree every generation, assuming Mendelian inheritance, so that each descendant receives one allele selected randomly from its mother and one from its father. Many iterations (typically 10 000) are performed to simulate sampling broadly throughout each individual's genome. (Each iteration can be thought of as representing stochastic Mendelian events at a different locus.) Gene drop models assume independence between model runs, thus no linkage, and no selection (Haig and Ballou 2002). These assumptions are untrue to whatever extent linkage and selection occur in particular genetic systems in real organisms.

Heterozygosity. Heterozygosity (H) is calculated from gene drop models by counting the allele frequencies of the founder alleles in the living extant population each simulation, averaging frequencies over simulations to obtain average allele frequencies (p_i) and estimating H using the formula for expected heterozygosity: $H = 1 - \Sigma p_i^2$. Thus, heterozygosity is interpreted as the proportion of the base population's heterozygosity retained in the extant captive population. This relative or proportional heterozygosity is often referred to as gene diversity in the captive-breeding literature (Lacy 1989). H as calculated in pedigree analysis is not directly relatable to molecular estimates of heterozygosity because it is proportional to expected heterozygosity in the base population (i.e., if $H = 0.90$, then the population has 90% of the base population's heterozygosity, whatever that might have been).

Founder genome equivalents. A useful concept related to retained heterozygosity is founder genome equivalents (f_g). This is the number of unrelated founders needed to establish a new population with the same levels of heterozygosity as that in the present population and is calculated as $1/[2(1 - H)]$. Thus, for example, a population with $H = 0.9$ has 5 founder genome equivalents; only five unrelated founders would be needed to establish a population with an initial $H = 0.9$ (Lacy 1989, 1995).

Founder allele survival. The proportion of a founder's genome that survives to the extant population (''allele retention,'' or r) is also calculated using gene drop models (Thompson 1986, Lacy 1989). A founder that produces only one offspring in the extant population has 50% allele retention because only one-half of its genes have been passed on to the single offspring. Founders with more complex descendant pedigrees will show more or less retention depending on the exact structure of their descendant's pedigrees. Founder allele survival is calculated as the proportion of a founder's two alleles that are present in the extant population. There are only three possibilities for a founder in any given simulation: neither allele present = 0%, only one present = 50%, both present = 100%; these are averaged over all simulations (Lacy 1989, Thompson 1986).

Mean kinship and inbreeding. Mean kinship is used to identify genetically important individuals. Mean kinship (mk_i) is calculated for every living animal in the population as the average kinship between that individual and all individuals in the population, including itself (Ballou and Lacy 1995). Individuals with low mean kinship have fewer or less-closely related relatives than those with high mean kinships. Ballou and Lacy (1995) showed that breeding strategies that preferentially select animals with low mean kinships are the best at retaining expected heterozygosity in the population, since average mean kinship is directly related to expected heterozy-

gosity ($H = 1 - \overline{mk}$). Thus, minimizing average mean kinship in the population maximizes heterozygosity. Most, if not all, captive-breeding programs now use mean kinship when selecting animals to breed (Ballou and Foose 1996).

Inbreeding coefficients (F) measure the degree of kinship between the parents of an individual and are calculated as the probability that an individual will receive two alleles that are identical by descent from the base population (i.e., two copies of the same founder allele; Falconer and Mackay 1996). Unrelated parents produce offspring with $F = 0$, while brother-sister, mother-son or father-daughter pairs produce offspring with $F = 0.25$. Both mean kinships and inbreeding coefficients are calculated directly from the pedigree using an additive relatedness matrix (Ballou 1983) rather than gene drop.

DATA

The data needed for population management, including births, deaths, parentage, and location of each individual, are recorded in the California Condor Studbook, currently maintained by Michael Mace at the San Diego Wild Animal Park (Mace 2002). Studbook data change constantly as individuals hatch, die, are moved between captive locations, or are reintroduced to the wild. We analyzed studbook data as of 21 August 2002, but modified those data by assuming scheduled transfers to new locations had already taken place. In general, we refer to individual condors by their studbook numbers. In some cases, we also provide names to facilitate comparisons with other sources on the population (e.g., Snyder and Snyder 2000).

INCORPORATING CLAN STRUCTURE INTO THE PEDIGREE

The relationships among some of the first 27 California Condors in the captive-breeding program were known from observations in the wild (Fig. 1). Birds identified as studbook numbers 2, 3, 4, 8, 9, and 10 were never brought into captivity but were known to be the parents of some that were (e.g., as eggs) and are therefore included in the studbook. The known pedigree relationships suggested that the population descended from 14 individuals (Fig. 1). We call these 14 individuals the ''apparent founders'' (marked by asterisks in Fig. 1). However, DNA fingerprinting indicated that the captive condors fell into three basic groups or clans (Geyer et al. 1993). Birds within clans were more closely related to each other than birds belonging to different clans. Although Geyer et al. (1993) could not determine the absolute level of relatedness among clan members with high accuracy, it was clear from their analysis that any captive-breeding strategy designed to maintain genetic diversity would need to incorporate the information on clan structure.

To incorporate the clan structure into the pedigree prior to analysis, we modified some studbook data to create an analytical studbook that we used for all analyses (Geyer et al. 1993; Fig. 1). For analytical purposes, we therefore assumed that birds within a clan had a coefficient of kinship of 0.125 (half-sibs), unless known otherwise from recorded pedigree information, and that kinship coefficients were 0 for individuals belonging to different clans. Assuming half-sib relationships among clan members is not unrealistic, given the California Condor's known history of small population size before the last birds were brought into captivity.

To establish these levels of relationships among the apparent founder birds in the studbook, we created hypothetical parents for them (Fig. 1). Each wild-caught bird within a clan was given a common hypothetical sire (i.e., HA, HB, or HC) and a unique hypothetical dam (e.g., H1, H2, etc, where the number was the same as the studbook number of the wild-caught individual). This structure achieved the desired result of members within a clan having kinships of 0.125, but kinships between clans being 0. By adding these hypothetical parentages, we increased the number of founders that contributed to the captive population. The population now had 17 founders (a unique dam for each apparent founder plus three added sires; Fig. 1). We call these 17 individuals the ''analytical'' founders.

ANALYSES

Analyses were conducted using SPARKS Studbook Management software (ISIS 1994); PM2000 version 1.16 (Pollak et al. 2002), MateRx version 1.9 (Ballou et al. 2001) and METAMK (Ballou 1999). PM2000 was used to evaluate the current demographic and genetic status of the total population. The probability that individuals carried the putative chondrodystrophy allele was calculated based on the pedigree for this trait given in Ralls et al. (2000).

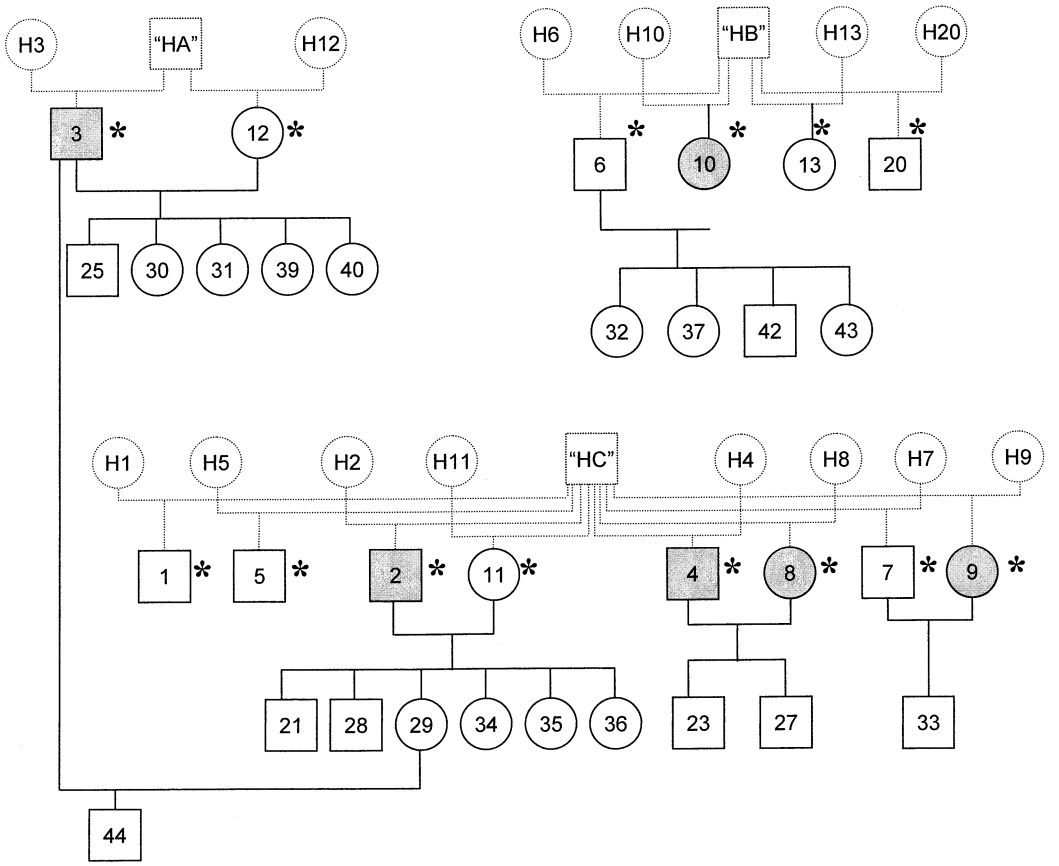

FIGURE 1. Pedigree of the 33 California Condors at the beginning of the captive breeding program. The 14 ''apparent founders'' are marked with an asterisk. The 17 ''analytical founders,'' added to define the hypothesized clan relationships among condors based on molecular analysis, are shown with dotted lines. Birds that died in the wild before being brought into the captive-breeding program are shaded.

PM2000 was also used to compare the genetic structure of various subpopulations. The proportion of founders' alleles remaining in each subpopulation was estimated by conducting a gene drop analysis for each subpopulation. The maximum proportion of each founder's alleles retained (r_{max}) is determined by the number of offspring produced (n): $r_{max} = 1 - 0.5^n$. Since the hypothetical dams (H1, H2, H3, . . . , H20) produced only one offspring each (the actual founders 1, 2, 3, . . . , 20), their maximum is 0.5. Since the hypothetical sires (HA, HB, HC) produced two, four and eight F_1 offspring, respectively, their maximum potentials are 0.75, 0.94 and 0.99.

Several other programs were used for the analyses to assist with 2002 management needs. We used MateRx to evaluate the genetic value of existing pairs. This program calculates a single numeric index for every male-female pair in the population that indicates the relative genetic benefit or detriment to the population of breeding that particular pair (Ballou et al. 2001). This index, the mate suitability index, is calculated from considering the pair's mean kinship, the difference in the male's and female's mean kinship, the inbreeding coefficient of the offspring that would be produced, and the amount of unknown ancestry in the pair. (At present, the condor population does not contain living individuals with unknown ancestry.) MateRx is designed to simplify the decisions about which pairs should be bred by condensing all that is known about the genetics of a pair into a single number. Mate suitability indices are labeled as beneficial (1, 2, or 3) indicating most to margin-

ally beneficial, or detrimental (4, 5, or 6, indicating slightly to highly detrimental) to the population, while ''—'' indicates that the pairing should not be considered in any case as the kinship of the pair, and the inbreeding coefficient of any offspring produced, is greater than 0.125. Beneficial mate suitability indices denote no detrimental effects relative to the genetic values of that pair, and 4, 5, or 6 indicate at least one detrimental effect.

MateRx was used with the default settings except for the definitions of bins used to evaluate the effect of differences in mean kinship between males and females. Initial modeling suggested that the default settings in MateRx might overcompensate for differences in mean kinship and label as detrimental pairs that would otherwise be considered suitable (R. Lacy, pers. comm.), particularly when all females are being bred, as is the case here. We therefore recalibrated MateRx so that pairs with differences in mean kinship less than 1.5% were defined as suitable (with differences less than 0.5%, less than 1.0% and less than 1.5% given ranks 1, 2, and 3 respectively) and differences greater than 1.5% as detrimental (with differences greater than 1.5%, 2.0%, and 2.5% receiving ranks 4, 5, and 6 respectively).

We also used MateRx to choose new pairs. First, we ranked the females available for pairing in order from lowest (most genetically valuable) to highest (least genetically valuable) mean kinship. For each female, we then listed four or more males that would be suitable mates in terms of producing the lowest possible mate suitability indices for the resulting pair. Many males were suitable mates for more than one female, so we noted their current location as well. We then chose the best mate available for each female, beginning with the most genetically valuable female at the top of the list. If pairing with more than one male would produce the same mate suitability index, we chose a male at the same location as the female to minimize the number of individuals that would have to be moved from one institution to another. We avoided choosing pairs that likely would be behaviorally incompatible, for example a very dominant female with a young, sexually inexperienced male, in the opinion of those familiar with the individual birds. We also avoided pairings that would have a high probability of producing a chick with chondrodystrophy (Ralls et al. 2000). Once we had selected a male for a given female, we crossed that male off as a possibility for all other females lower down on the mean kinship list.

We selected pairs to be sent to the new facility at the Oregon Zoo based partly on availability and partly on genetic background. METAMK (Ballou 1997) was used to select a genetically diverse set of pairs. METAMK uses changes in mean kinships to calculate the increase or decrease in heterozygosity for both a source and destination population when a specific individual is moved from one to the other (Ballou 1997). In this case, the source population is the entire captive population and the destination population is Oregon Zoo. The first pair was chosen on the basis of minimizing genetic loss to the existing captive population and subsequent pairs were selected iteratively partly on the basis of their low level of relatedness to birds already chosen to go to Oregon, and partly on availability (i.e., not already paired up).

''Mentors'' are adult or nearly adult birds that are placed with groups of captive-born chicks to help them develop appropriate social behavior and fear of humans. Mentors were evaluated on the basis of mean kinship as calculated by PM 2000 (Pollak et al. 2002). Because mentors are not used for breeding, they should be selected from the less genetically valuable individuals, that is, those with high mean kinship.

METAMK was also used to make recommendations regarding which chicks should be retained in the captive (source) population and which should be reintroduced to the wild (the destination population). Haig and Ballou (2002) illustrated this procedure using data for golden lion tamarins (*Leontopithecus rosalia*). METAMK was again used to recommend which of the chicks to be reintroduced should be released in California and which should be released in Arizona. First, we assumed that all chicks to be reintroduced were part of the wild California population. METAMK then provided data on the genetic costs and benefits (i.e., increase or decrease in heterozygosity) of either keeping that chick in the wild California population, or transferring it to Arizona. Placement of chicks was determined by the effect on overall heterozygosity (average change in H in California and Arizona caused by transferring the chick).

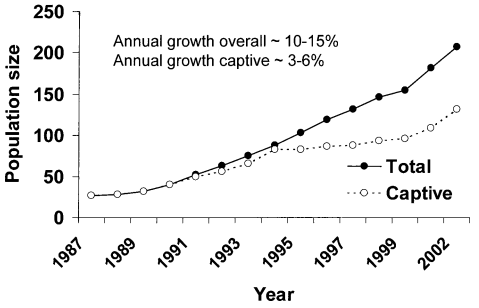

FIGURE 2. Growth of the California Condor population since captive breeding began in 1987 showing both the total number of birds at the end of each year and the number in captivity.

RESULTS

STATUS OF THE POPULATION AND ITS SUBPOPULATIONS

Demography. There were 206 birds in the population on 21 August 2002, with 113 in captivity and 93 in the wild. The captive birds were distributed among three facilities: 32 at the Los Angeles Zoo, 35 at the San Diego Wild Animal Park, and 46 at the World Center for Birds of Prey in Boise, Idaho. The wild birds were divided into three subpopulations: 50 in California, 37 in Arizona, and 6 in Baja California, Mexico. Growth of the total population has been between 10% and 15% per year since 1987 (Fig. 2), when the last wild birds were brought into captivity. Since 1992, the growth of the captive population has been only about 5% per year due to the removal of chicks for reintroduction each year.

The age structure of the current population is relatively young because the captive population has been in existence only since the late 1980s. Most birds older than about 14 years are wild-caught birds and their ages are estimates. Overall, there is a balance between males and females, and the age structure is typical of a rapidly growing population (Fig. 3a). The wild population consists mostly of young birds and a few adults that have recently attained sexual maturity (at 5–6 years of age; Fig. 3b). The age structure of the captive population (Fig. 3c) shows a deficit of animals in age classes 1–4 years because almost all chicks for the last 5 years have been reintroduced.

Given management goals and the current demography of the population, it is still appropriate to breed all adult females in captivity to increase the size of the population as rapidly as possible and provide chicks for reintroduction. There is also a need to begin retaining some chicks in captivity to rectify the deficit of younger individuals in the captive population.

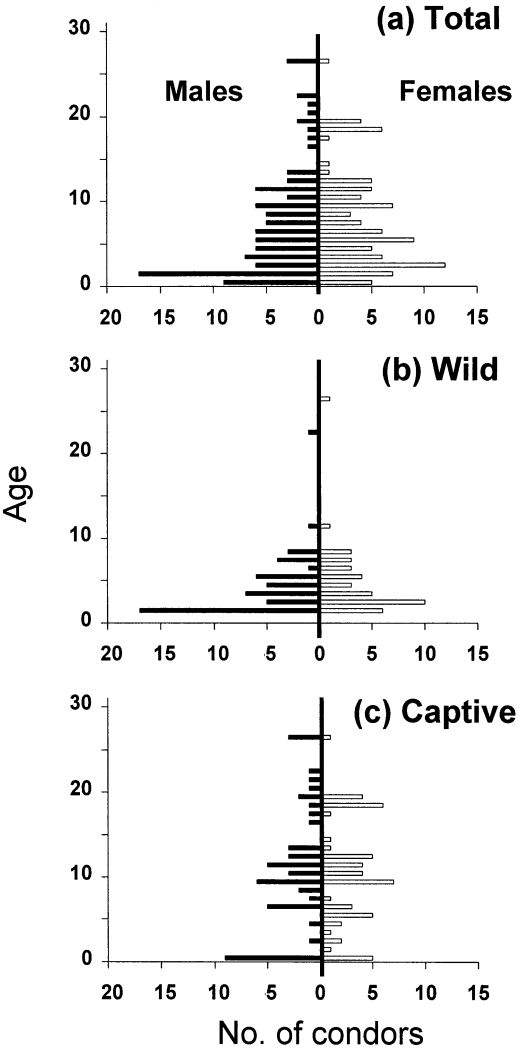

FIGURE 3. Age structures of the (a) total, (b) wild and (c) captive California Condor populations.

Genetic analyses. Any assumption that the 14 apparent founders are related in some way will result in an immediate loss of heterozygosity in the captive population compared to the amount that would have been present if the founders had been unrelated. Our assumption that the birds within clans were half-sibs resulted in an average kinship of 8% among the 14 apparent founders, meaning that on average they were slightly more related to each other than cousins (Table

TABLE 1. Summary of California Condor population genetics. Retained heterozygosity is the estimated proportion of the heterozygosity of the wild California Condor population prior to its bottleneck that is retained in the present-day population. Founder genome equivalents are the number of unrelated founders that would be needed to establish a population with the same level of retained heterozygosity as shown in the population.

Genetic characteristics	Apparent founders (n = 14)	Current population (n = 206)	Captive population (n = 113)	Wild population		
				Arizona (n = 37)	California (n = 50)	Total (n = 93)[a]
No. analytical founders represented	17	17	17	16	16	17
Proportion heterozygosity retained	0.920	0.914	0.915	0.897	0.901	0.901
Founder genome equivalents	6.2	5.8	5.9	4.9	5.0	5.4
Mean inbreeding	0.00	0.03	0.04	0.01	0.02	0.02

[a] Includes six condors in Baja California.

1). Under this assumption, the birds used to found the captive population contained only 92% of the heterozygosity contained in the hypothetical wild base population prior to its bottleneck (Table 1). This equates to 6.2 founder genome equivalents. In the current population, (wild and captive combined) heterozygosity is 91.4%, down only slightly from the 92.0% of the founders (Table 1). Thus about 99.5% of the heterozygosity that the founders brought into the population has been retained in the current population. This is because condors are long-lived and the captive population has been under genetic management since its inception.

The average mean kinship for the total population is 0.086 with individual mean kinships ranging from 0.067 to 0.108 (Fig. 4). A mean kinship of 0.063 is equivalent to an individual being related to the population on average at the level of first cousin; a mean kinship of 0.125 is comparable to half-sibs. While all birds should be bred, birds with mean kinships below the average should be given the highest breeding priority. This applies, in particular, to the three birds with the lowest mean kinships (birds 1, 5, and 33; Fig. 4).

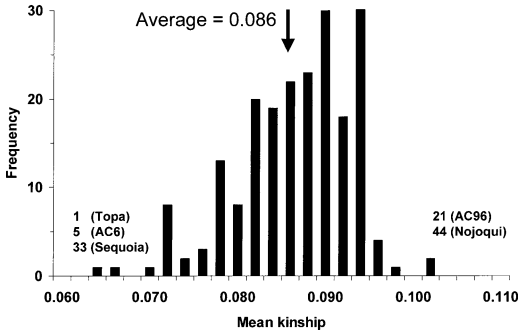

FIGURE 4. Frequency distribution of mean kinship values in the living population of California Condors. Average mean kinship is 0.086. The three birds with the lowest mean kinship (most valuable) and the two with the highest (least genetically valuable) are identified.

The frequency distribution of the probability of carrying the putative chondrodystrophy allele (Ralls et al. 2000) for the total population is shown in Figure 5. The average probability of being a carrier is 18%, although there are only two living birds that are known to be carriers (27 and 31; the parents of four of the five chondrodystrophic chicks produced so far). However, there are many birds with at least a one-in-three chance of being a carrier.

Genetic structure in the subpopulations. Retained heterozygosity is somewhat lower in the wild than in captivity (Table 1), which is not surprising since some of the more genetically valuable animals and their descendants have not

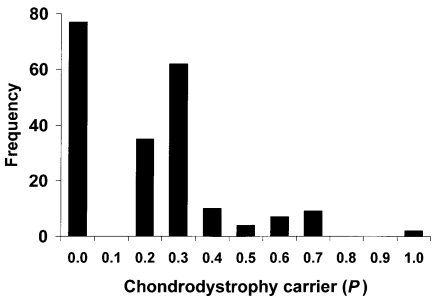

FIGURE 5. Frequency distribution of the probability of an individual California Condor carrying the lethal chondrodystrophy allele. All 206 living birds are included. Two birds are known carriers (P = 1.0).

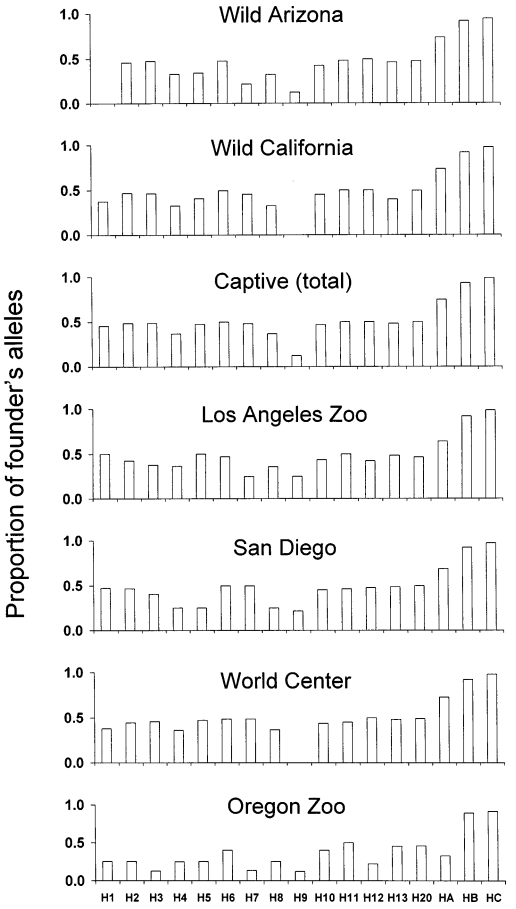

FIGURE 6. Proportion of founders' alleles present in subdivisions of the California Condor population. San Diego refers to the San Diego Wild Animal Park and World Center refers to the World Center for Birds of Prey in Boise, Idaho. Alleles from analytical founder H1 are missing in Arizona and alleles from founder H9 are missing in California and the World Center.

yet been reintroduced. The level of inbreeding is less in the wild because only non-inbred birds have been reintroduced and wild birds have yet to breed.

There are only small to moderate differences between the wild populations in California and Arizona based on heterozygosity (Table 1). F_{ST}, a common measure of genetic differences between populations (Frankham et al. 2002), is only 0.009, indicating only minor differences in the frequency of founder alleles in the two populations. We did not evaluate the wild population in Baja California because it was established with only six birds in 2002.

A more detailed genetic comparison of the wild populations in California and Arizona is provided by estimates of the proportion of each analytical founder's alleles that are present in each population (Fig. 6). The most obvious difference between these two subpopulations is that alleles from bird number 1 (''Topa'') are missing from the Arizona population, and alleles from bird 9 are missing from the California population. Number 1 is still alive and reproducing but 9 is dead. Its alleles are represented in the population through its offspring, 33 (''Sequoia''). Condor number 7 (''AC5'') is also underrepresented in the Arizona population.

The founders' alleles also are fairly well distributed between the three current breeding facilities (Los Angeles, San Diego Wild Animal Park, and World Center for Birds of Prey; Fig. 6), although the World Center for Birds of Prey lacks alleles from condor 9. Genetic deficits in specific wild or captive populations can be rectified by moving individuals carrying alleles from the underrepresented founders to the appropriate location.

MANAGEMENT RECOMMENDATIONS FOR 2002

Genetic evaluation of existing pairs. We evaluated the genetic value of all current pairs in the population by calculating mate suitability indi-

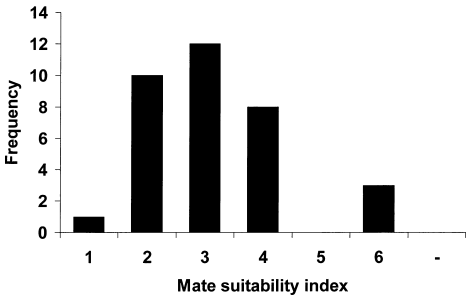

FIGURE 7. Frequency distribution of the mate suitability indices for the 34 condor pairings prior to the 2002 genetic management recommendations. Mate suitability index scores of 1, 2, or 3 indicate mostly to marginally beneficial pairs. Scores of 4, 5, or 6, indicate slightly to highly detrimental pairs for maintaining genetic diversity in the population. Pairs receiving a ''—'' should not be considered in any case because the kinship of the pair, and the inbreeding coefficient of any offspring produced, would be greater than 0.125. The three highly undesirable pairings (with scores of 6) were broken up and the individuals repaired with other birds.

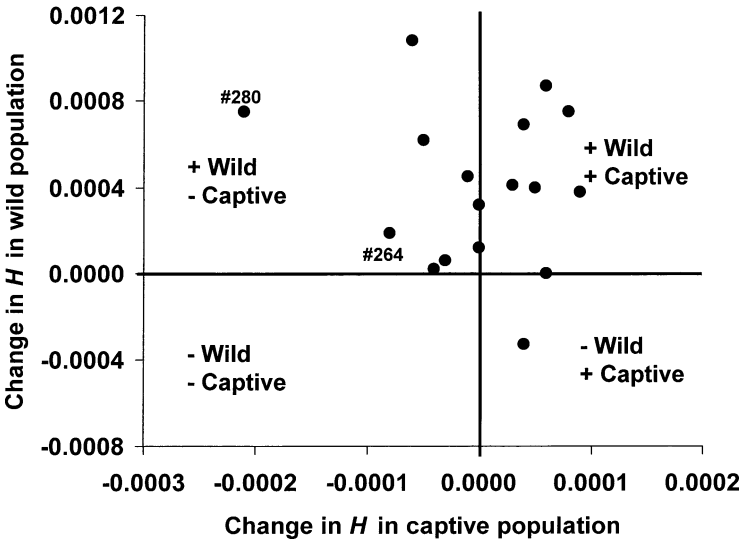

FIGURE 8. Expected changes in heterozygosity in the captive and wild California Condor populations resulting from reintroducing individual captive chicks into the wild. Each point shows the negative or positive change in heterozygosity in the captive and wild population if that individual were to be reintroduced.

ces for each pair (Fig. 7). Three existing pairs were judged genetically detrimental, with a mate suitability index of 6: individuals 20 and 29, 44 and 45, and 33 and 79. These pairs were detrimental because a bird with a very low mean kinship was paired with a bird with a very high mean kinship. Such matings are undesirable because they link rare alleles with overrepresented alleles in any offspring (Ballou and Foose 1996).

Choosing new pairs. The pool of individuals available for pairing included those from the three pairs with high mate suitability indices that needed to be re-paired, those from four pairs that appeared incompatible based on poor reproductive performance and behavioral observations, and all unpaired captive birds of breeding age except for mentors. The pairing procedure based on mean kinship resulted in 11 new pairs for a total of 39 potentially breeding pairs. No males were available for the remaining five females, all of which had high mean kinships and thus were judged suitable for uses other than breeding, such as placement in exhibits or use as mentors.

Genetic evaluation of mentors. Genetic review of the existing mentors indicated that two birds, 63 and 64, had mean kinships that fell in the high end of the distribution and were appropriate for long-term use as mentors (as opposed to breeders). However three others, 138, 140, and 141, had lower mean kinships (in the low end of the distribution) and should be used in the captive-breeding program sometime in the future once replacement mentors are developed. Three less genetically valuable birds, 36, 59, and 79, were identified as possible new mentors.

Creating a new captive population. We selected six pairs to begin the new captive population at the Oregon Zoo. While all founders are represented (Fig. 6), less than 25% of the genome is represented for the majority of founders. This is to be expected given this small number of individuals and can be improved by the addition of pairs as they become available.

Placing the 2002 chicks. Decisions as to which birds to release in Baja California were made prior to our analyses based on chick-rearing methods (all birds released in Baja California are to have been reared in the same manner, using a revised protocol for puppet rearing plus exposure to mentors; M. Wallace, pers. comm.). The age structure of the captive population (Fig. 3c) indicated that it was advisable to retain some chicks in the captive population. We recommended retaining the two chicks genetically most valuable to the captive population, 280 and 264 (Fig. 8).

The remaining chicks were to be released in either Arizona or California depending on their genetic value in those populations. Seven chicks

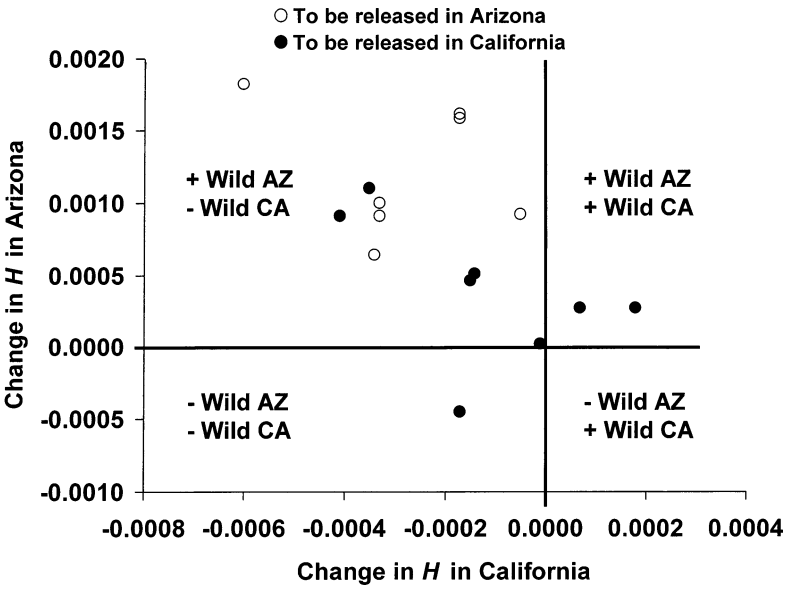

FIGURE 9. Effect on heterozygosity of placing California Condor chicks in the Arizona or California wild populations. For analytical purposes, each chick was initially placed in the California population. Each point shows the negative or positive change in heterozygosity in the Arizona and California wild populations if that individual were to be transferred from California to Arizona.

were selected for release in Arizona and 10 in California (Fig. 9). It was not possible to avoid some slightly negative genetic effects: all chicks scheduled for release in Arizona would have a positive genetic effect on that population if they survived and bred, but some of the chicks scheduled to be released in California would have a slightly negative effect on that population. However, placement of all chicks improved the overall gene diversity in the total population.

DISCUSSION

The California Condor population has suffered a severe population bottleneck, at one point declining to only 27 individuals descended from 14 apparent founders. The deleterious genetic effects of this bottleneck include increased mean kinship and loss of heterozygosity, loss of alleles, small effective population size, and increases in deleterious alleles due to founder effects. Our assumption, based on molecular genetics, that kinship within clans was 12.5% resulted in about an 8% loss of expected heterozygosity before the last condor was taken into captivity in 1987. Although the significance of an 8% loss of heterozygosity in any species is unknown, heterozygosity loss tends to be associated with decreased survival, reproductive success, and lifespan (Frankham et al. 2002). Nevertheless, there are some wild populations with very little heterozygosity, such as island foxes (*Urocyon littoralis*; Wayne et al. 1991), southern elephant seals (*Mirounga angustirostris*, Hoelzel et al. 1993) and even Andean Condors (*Vultur gryphus*, Hendrickson et al. 2003). Because alleles and mitochondrial DNA lineages are lost more rapidly than heterozygosity (Allendorf 1986), the California Condor population also has lost some of these types of genetic diversity. Loss of alleles is significant because it lessens the ability of a population to adapt to changed selection pressures (Allendorf 1986). Chemnick et al. 2000 have documented the loss of two of four mitochondrial lineages known from the remnant wild population of condors, but the significance of this is unknown.

The high frequency of the lethal chondrodystrophy allele in the condor population is probably another result of the population bottleneck (Ryder 1988, Laikre et al. 1993, Ralls et al. 2000). Such deleterious alleles are rare in large, normally outbreeding populations, but those that pass through a bottleneck will increase to a frequency of at least $1/(2N)$ after the bottleneck (where N is the effective size of the bottleneck; Frankham et al. 2002).

Even with the current 13% growth rate, the condor population will continue to have a small effective population size for many years. This will have two effects. First, the small size will further compromise its ability to adapt to changes because evolution in small populations (i.e., effective population sizes <200) is determined primarily by genetic drift rather than adaptation through natural selection (Frankham et al. 2002). Second, the condor population is still small enough that some continuing loss of genetic diversity through genetic drift is unavoidable (Frankham et al. 2002). Genetic diversity will be lost more slowly as population size increases but will continue until the population reaches a size where this loss is balanced by gains in diversity produced through new mutation ($N_e \sim 500$; Franklin and Frankham 1998).

Careful genetic management since the last birds were taken into captivity has minimized further losses of heterozygosity and founder alleles. Careful placement of animals has also assured that the remaining genetic diversity of the species is well distributed across the three captive-breeding facilities and the California and Arizona reintroduction sites to protect against catastrophic loss of genetic diversity due to disasters such as fires or disease epidemics at any one site. Additional molecular-genetic studies promise to refine existing management techniques. Current assumptions regarding the relationship among the 14 apparent founders based on DNA fingerprinting (Geyer et al. 1993) should be improved by ongoing analyses of microsatellite data (O. Ryder, pers. comm.) as was recently accomplished for Whooping Cranes (*Grus americana*; Jones et al. 2002).

Molecular techniques also have the potential to improve management for the chondrodystrophy allele by developing a technique to identify carriers. The chondrodystrophy trait in condors appears to be the same as the autosomal recessive chondrodystrophy trait identified in chickens (*Gallus gallus*), a species whose genetics have been studied extensively. Raudsepp et al. (2002) used cytogenetic screening to compare condor and chicken genomes to identify homologous genomic regions, which will facilitate the use of the chicken genome to identify markers associated with the chondrodystrophy allele.

The current genetic status of the condor population compares favorably with that of other species that have been rescued from extinction by captive breeding. The condor population is descended from 17 analytical founders and has an average mean kinship of about 8%. The black-footed ferret (*Mustela nigripes*) population of over 300 individuals is descended from only seven analytical founders and has an average mean kinship of about 12.5% (Marinari 2001, Wisely et al. 2003). The current population of over 200 Guam Rails (*Rallus owstoni*) is descended from only 10 analytical founders and has an average mean kinship of about 9% (Orndorff 1999). Captive-breeding programs for all three species were genetically handicapped from the start because captive populations were not initiated until only a few individuals of the species remained. The World Conservation Union recommends establishing captive populations when wild populations drop below 1000, rather than waiting until the last minute (IUCN 1987). This allows captive populations to begin with an adequate number of founders (25–30) to retain the full genetic diversity of the wild population (Soulé et al. 1986, Frankham et al. 2002).

Since the last wild birds were taken into captivity in 1987, the genetic status of the California Condor population has been strongly influenced by management decisions. This situation will continue for many years until reproduction in the wild populations exceeds that in the captive population. However, as individuals in the wild populations mature and choose their own mates, some birds will undoubtedly mate with close relatives due to lack of other alternatives. Production of inbred chicks will lead to increased expression of deleterious alleles, such as that for chondrodystrophy, in the wild populations. Additional deleterious alleles are likely to be discovered in the condor population once inbreeding occurs in the wild because inbreeding avoidance in the captive population has minimized the expression of such alleles.

If the current 13% growth rate continues, the condor population will reach 450 individuals, the provisional threshold for downlisting the species from endangered to threatened (USFWS 1996), in about 7 years. The recovery plan (USFWS 1996) specifies that there must be at least three populations of 150 birds, one captive and two wild, before downlisting can be considered. Even at these population sizes, condors will continue to lose genetic diversity. Effective population sizes are always smaller than actual population sizes, averaging around 30% of ac-

tual population size in genetically managed captive populations (Frankham et al. 2002) and around 11% of population size in the wild (Frankham 1995). If we use these estimates, the three condor populations specified in the recovery plan would have effective population sizes of 45, 15, and 15. If maintained at this level without further reintroductions and transfers among the subpopulations, condors would lose genetic diversity at the rate of $1/(2N_e)$ (Nei et al. 1975), become increasingly inbred at between 1% (captive) and 3% (wild) per generation, and be related at the level of full siblings (0.25) in six (wild) and 17 (captive) generations.

Furthermore, theory and data on a variety of organisms ranging from plants to mammals (Frankham et al. 2002), including case studies on birds (e.g., Keller and Waller 2002), suggest that a 0.25 level of inbreeding would be high enough to directly reduce fitness even in the absence of detectable genetic abnormalities. Thus, it will be important to continue increasing total population size and interactive genetic management of the wild and captive California Condor populations even after the provisional downlisting criteria are reached.

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