



FEATURE ARTICLES

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LOW GENETIC VARIABILITY IN THE GEOGRAPHICALLY WIDESPREAD ANDEAN CONDOR

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Abstract. We characterized DNA sequence variation in the mitochondrial control region and 12S ribosomal subunit for a sample of Andean Condors (*Vultur gryphus*) representing populations distributed throughout the species' extensive geographic range (Colombia to central Argentina and Chile). Domains II and III of the control region along with part of the 12S gene were sequenced from 38 individuals (956 base pairs in 30 individuals and 430–824 base pairs for an additional 8 individuals sampled from museum specimens), and Domain I was sequenced from five of these birds (400 base pairs). We identified a total of five haplotypes based on four variable sites distributed over Domains II and III of the control region and the 12S gene. An additional variable site was identified in Domain I. All changes were transitions and no more than three sites differed between any two individuals. Variation in the control region of condors was lower than for most other birds analyzed for these loci. Although low genetic variability is often associated with endangered megafauna, the condor example is notable because the species still maintains a substantial geographic range. Thus, low genetic variability may occur even in megafauna whose ranges have not been severely reduced over recent centuries. Our results therefore suggest that genetic data from geographically widespread megafauna provide important baseline data for assessing the relationship between genetic variability and its causes in other endangered species.

Key words: *Andean Condor, Cathartidae, control region, mitochondria, Vultur gryphus.*

Baja Variabilidad Genética en Poblaciones de *Vultur gryphus* con Amplia Distribución Geográfica

Resumen. Caracterizamos la variación de la secuencia de ADN en la región de control mitocondrial y la subunidad ribosomal 12S en una muestra de *Vultur gryphus* representativa de poblaciones distribuidas a lo largo del extenso rango geográfico de la especie (Colombia, hasta el centro de Argentina y Chile). Los dominios II y III de la región de control, junto con parte del gen 12S, fueron secuenciados en 38 individuos (956 pares de base en 30 individuos y 430–824 pares de base para una muestra adicional de 8 especímenes de museo), y el dominio I fue secuenciado en 5 de estas aves (400 pares de base). Identificamos un total de cinco haplotipos basados en cuatro sitios variables en los dominios II y III de la región de control y el gen 12S. Un sitio variable adicional fue identificado en el dominio I. Todos los cambios fueron transiciones y entre dos individuos cualesquiera no variaron más de 3 sitios. La variación en la región de control de los cóndores fue más baja que para la mayoría de las aves analizadas para estos mismos loci. Aunque la baja variabilidad genética es a menudo asociada con megafauna en peligro de extinción, el ejemplo del cóndor es notable porque la especie aún mantiene un rango geográfico substancial. Así, la baja

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variabilidad genética se puede dar incluso en la megafauna cuya dispersión no haya sido sujeta a severas reducciones en los últimos siglos. Por lo tanto, nuestros resultados sugieren que los datos genéticos de rapaces con amplia distribución geográfica y de otra megafauna proveen de importante información de base para evaluar la relación existente entre la variabilidad genética y sus causas en otra megafauna en peligro.

INTRODUCTION

In many genetic studies of endangered species, baseline data on the levels of genetic variability that existed before the species became rare are lacking. Such data provide important controls for interpreting possible consequences of population declines such as loss of genetic diversity (Glenn et al. 1999) or inbreeding depression (Charlesworth and Charlesworth 1987, Eldridge et al. 1999). Knowledge of genetic variability in natural populations appears important in particular for interpreting the conservation status of large-bodied organisms, which are sensitive to population declines (Diamond 1984, Belovsky 1987). Recent studies imply that levels of genetic variation may be inversely related to body size and its associated life history attributes. Specifically, taxa as diverse as whales (Hoelzel and Dover 1991, Murray et al. 1995), bears (Allendorf et al. 1979, Cronin et al. 1991, Paetkau and Strobeck 1994), and big cats (Winkler et al. 1990, Roelke et al. 1993) among mammals, and large raptors (Bald Eagle [*Haliaeetus leucocephalus*]: Morizot et al. 1985, Spotted Owl [*Strix occidentalis*]: Barrowclough and Gutiérrez 1990, Spanish Imperial Eagle [*Aquila adalberti*]: Negro and Hiraldo 1994, Japanese Golden Eagle [*Aquila chrysaetos japonica*]: Masuda et al. 1998, Bearded Vulture [*Gypaetus barbatus*]: Negro and Torres 1999) among birds all express low variability despite widely different population histories.

Because so many species of megafauna are threatened, it is difficult to find a suitable study species in which to examine genetic variability in the absence of dramatic population declines. The Andean Condor (*Vultur gryphus*) provides a rare opportunity to study a large-bodied, threatened species, for three reasons. First, condors represent the extreme for many physical and demographic characteristics among living birds including wingspan, weight, and generation time. Second, the Andean Condor still maintains a substantial geographic range throughout western South America from Colombia to Tierra del Fuego, providing an opportunity to examine levels of genetic variability in a

large-bodied species across an extensive area. Third, two distinct population structures are expressed in different parts of the condor range, allowing for an internal comparison of the effects of population structure on genetic variability. In the Andes of Colombia and Ecuador (and formerly Venezuela before extirpation of the wild population), condors reside in the páramo, a highly fragmented system of Andean peaks. Population density is low, and changes in condor numbers throughout the last century suggest that populations in the north are susceptible to decline. By comparison, south of the Northern Peruvian Low in Cajamarca, condors reside in the more continuous highland puna, coastal, and desert habitats where they achieve population densities higher than in the north. The shift in physical geography at the Northern Peruvian Low, which influences population structure in many taxa (Vuilleumier 1969, Parker et al. 1985), makes it possible to compare variability between areas north and south of the low.

To characterize genetic variation within and among Andean Condor populations, we examined mitochondrial DNA sequences from the control region and the 12S ribosomal subunit genes. The control region is well suited to address questions about variability because it expresses a high level of genetic polymorphism across a wide range of taxa. Thus, evidence for low variability in condors should be readily detected.

METHODS

SAMPLES

Tissue or blood samples from wild condors are difficult to obtain because the species is carefully protected throughout its range; therefore, genetic samples were obtained from birds in zoos and recovery programs, museum specimens, and salvage feathers collected in the wild. Captive birds used for sources of blood and feathers were all wild-caught individuals from known capture localities. To incorporate changes in biogeography throughout the condor range into the analysis, we obtained samples from both north (Ecuador, Colombia) and south (Peru, Bo-

livia, Chile, and Argentina) of the Northern Peruvian Low. Detailed locality information is given in the appendix.

DNA STORAGE AND EXTRACTION

Blood samples were stored in tubes containing EDTA at 0°C. Feather calami and museum skin samples were kept in sterile tubes at room temperature. Samples from museum specimens were obtained by cutting 1–2 cm² of skin from an apterium on the side of the body, where the specimen was unlikely to have been contaminated by human handling during preparation. QIAamp Tissue and Blood Kits (Qiagen, Inc., Valencia, California) were used for all DNA extractions following manufacturer's instructions with extended lysis times (2 hr for blood samples and overnight for skin and feather samples) and double the suggested amount of Proteinase K for dried skin and feather samples.

GENES AND PRIMERS

The control region is divided into three domains that evolve at different rates (Baker and Marshall 1997). Domains I and III are the most variable, and typically provide ample genetic markers for population-level studies. The 12S ribosomal RNA gene is located downstream from the control region, and is less variable because of functional constraints. Initially, long-PCR (Expand Long Template PCR System, Boehringer-Mannheim, Indianapolis, Indiana) was used to obtain sequence between the cytochrome *b* (primers designed from sequences in Siebold and Helbig 1995) and 12S genes of an Andean Condor. Gene order between cytochrome *b* and 12S in condors was found to be the same as in the chicken. A combination of chicken (H1795 and L543 [Quinn and Wilson 1993]) and condor-specific primers (L16652: 5'-CGAAACACACCCCGAGAAAAG-3'; H621: 5'-CGCGATCACGGACGAAAATGG-3'; L798: 5'-GCAGTTTGCTTTCCATTCG-3'; and H1455: 5'-GGCTGTGCAAGGTGTCTTG-3') designed from the original sequences were used to amplify the control region and 12S genes. The 956 base pairs (bp) of the second and third domains of the control region and the 12S gene were compared in 30 Andean Condors. These sequences were aligned using GCG (Genetics Computer Group 1998). Our inability to resolve the 5'-CAACAAA-3' repeats found at the 3' end of Domain III suggests that heteroplasmy occurs in condors

as it does in several other species in Ciconiiformes (Berg et al. 1995, Crochet and Desmarais 2000). Because of this, repeat sequences were removed from the analysis. Some DNA samples extracted from museum specimens were highly degraded; therefore, sequencing in an additional 8 Andean Condors was focused on regions in Domains II and III and 12S that contained variable sites determined in the original condor sample (individuals 44, 45 = 430 bp; 30, 31, 39, 42 = 590 bp; 41, 47 = 805 bp). Individuals without complete sequences were used only for analyses of geographic distribution of haplotypes, and were not included in diversity analyses (see below).

For five Andean Condors from disparate geographic locations (Argentina, *n* = 2; Peru, *n* = 1; Ecuador, *n* = 2) an additional 400 bp of sequence was obtained from Domain I of the control region, beginning 120 bp into the chicken control region (Desjardins and Morais 1990).

SEQUENCING

The polymerase chain reaction (PCR) was carried out in 100-μL volumes for 2 min at 94°C, followed by 40 cycles of 94°C for 1 min, 50°C for 1 min and 70°C for 1 min. PCR products were excised from 1% low-melting-point agarose (Promega, Inc., Madison Wisconsin), reamplified for better yield, and cleaned with the Wizard PCR preps DNA Purification System (Promega, Inc.) before sequencing with ABI Prism BigDye chemistry (PE Biosystems, Foster City, California) and run on a 4.5% acrylamide gel.

Nuclear copies of mitochondrial DNA found in some species of birds (Quinn 1992, Kidd and Friesen 1998) are a potential problem for variability estimations. Isolation of pure mitochondrial DNA was not possible for most samples in this study because of limited starting material; however, several factors support the mitochondrial origin of sequences studied. First, the use of long-PCR and subsequent design of taxon-specific primers avoids amplification of large, slowly evolving nuclear copies of mtDNA that can be preferentially amplified with cross-taxon primers (Sorenson and Quinn 1998). Second, the amount of sequence similarity between chicken and condor conserved regions is consistent with a mitochondrial origin because small fragments translocated to the nucleus typically evolve rapidly (Quinn 1992). Third, although a combina-

TABLE 1. Summary of the number of individuals compared and substitutions found for three regions of the Andean Condor mitochondrial genome. Only samples with complete sequences were used for diversity estimates. Nucleotide and haplotype diversity are reported as means \pm SD; n = number of individuals.

Gene region	n	No. of base pairs (n individuals)	No. of variable sites	Nucleotide diversity (π)	Haplotype diversity (h)
Control region					
Domain I	5	400	1	—	—
Domains II–III	38	501 (32), ≥ 250 (6) ^a	2	0.0020 ± 0.0016	0.59 ± 0.05
12S ribosome	38	434 (30), ≥ 140 (8) ^a	2	0.0006 ± 0.0007	0.25 ± 0.10

^a Numbers following the comma indicate number of base pairs amplified from variable regions only (n museum samples).

tion of tissue types was used to complete the analysis, PCR products were of uniform size and lacked any shadow bands in amplification products which may have resulted from the different mtDNA content of blood, feather, and skin.

STATISTICAL ANALYSES

Nucleotide (Nei and Li 1979) and haplotype (Nei and Tajima 1981) diversity were used to indicate levels of variability in condor populations. Tajima's D (1989a, 1989b) and the mismatch distribution (Rogers 1995) were used to test for departures from neutrality in the population. A Fisher's exact test was used to check for the differences in the frequency of alleles among the northern and southern Andean Condor populations. All of the prior analyses were performed in ARLEQUIN (Schneider et al. 2000).

To examine whether the haplotype number observed in the Andean Condor sample was lower than other species of birds for which comparable control region data were available from similar or larger sample sizes, we compared the observed number of haplotypes for each of the species with the number of haplotypes that would be expected at each sample size if the species had the same haplotype diversity as the Andean Condor, assuming a neutral, infinite-allele model (Ewens 1972). Although this neutral model may not be completely appropriate in this situation, it should provide a suitable approximation. This method allowed us to compare studies with different sample sizes. Haplotype diversity (h) was calculated as $(1 - \sum p_i^2)n/n - 1$, where p_i is the proportion of all haplotypes represented by the i th haplotype and n is the number of individuals in the sample (Nei and Tajima 1981). The expected number of alleles

$[E(k)]$ in a sample of n individuals according to a formula by Ewens (1972), modified for haploid mitochondria by Nei and Tajima (1981), was calculated as

$$E(k) = \frac{M}{M} + \frac{M}{M+1} + \dots + \frac{M}{M+n+1},$$

where $M = h/(1-h)$, and h is the haplotype diversity as defined above. All values are given as means \pm SD.

RESULTS

A total of five haplotypes was detected based on two variable sites identified in the control region (Domains II and III) and two in 12S within the Andean Condor sequences (Table 1). These sequences have been deposited in GenBank under accession numbers AY129644 to AY129649. Only a single additional variable site was found in the five sequences (representing four geographic localities) that included Domain I. All substitutions were transitions, and nucleotide (π) and haplotype (h) diversity estimates for the Andean Condor control region and 12S genes were low relative to other bird species. The slightly higher diversity values found in the control region compared to the more conserved 12S gene suggests that the mitochondrial genome is evolving in condors as would be expected based on the different constraints on each of the genes.

GEOGRAPHIC DISTRIBUTION OF HAPLOTYPES

Condor populations in both the northern páramo and the southern puna, coast, and desert areas had low genetic diversity (Table 2). Both regions had few haplotypes, and nucleotide and haplotype diversity did not differ greatly between the northern and southern samples. Thus it appears that diversity of mtDNA does not strongly re-

TABLE 2. Comparison of mitochondrial control region (Domains II and III) nucleotide (π), and haplotype (h) diversity estimates for Andean Condors from the northern versus the southern Andes. Nucleotide and haplotype diversity are reported as means \pm SD; n = number of individuals.

Region	n	No. of haplotypes	π	h
Northern páramo (Ecuador)	6	3	0.0010 \pm 0.0009	0.73 \pm 0.16
Southern puna, coast, and desert (Peru, Argentina, Chile)	24	4	0.0009 \pm 0.0007	0.65 \pm 0.07

flect the regional differences in ecology or degree of isolation, although larger sample sizes are needed to substantiate this conclusion.

Further evidence for low variability throughout the range comes from samples from two isolated areas in the condor's range, the Sierra Nevada de Santa Marta in coastal Colombia (Fig. 1, site 1) and in Sierra de Córdoba, the far eastern isolate of the Andes in central Argentina (Fig. 1, site 7). Although these isolated massifs are not located along the main Andean spine, condors from these areas showed no unique haplotypes. The haplotype present in the Sierra Nevada de Santa Marta was of the most common form, found also in Ecuador, Peru, and central Argentina. Similarly, the haplotype present in Sierra de Córdoba was the same as that found in the Andes of central Chile, directly to the west.

Even though overall diversity estimates were low, the frequency of each haplotype in regions north and south of the Northern Peruvian Low differed significantly ($P = 0.02$, exact test, two regions \times five haplotypes, $n = 38$). One haplotype was found only in the north, and two others were found only in the south (Fig. 2), indicating that some degree of differentiation between populations has occurred.

COMPARISONS TO OTHER AVIAN SPECIES

The diversity of mitochondrial genes in the Andean Condor appears to be low relative to outbred birds for which comparable data are available (Table 3). Using Ewens' (1972) model to compute expected number of haplotypes for each species based on the haplotype diversity of the Andean Condor, it is clear that the only species with close observed and expected values are those which have experienced a recent bottleneck, such as the Whooping Crane (Glenn et al. 1999), or those that show unusually low variability compared to conspecifics (Barrowclough et al. 1999). The observed number of alleles in

all other species was 2.4 to 5.3 times greater. Nucleotide diversity, which is less dependent on sample size or length of sequence examined, also showed that condors have low genetic variability compared to outbred populations. Moreover, if only the more variable Domain III were used for comparison, Andean Condors would show even greater disparity relative to other avian species, since they have no variability in this domain.

TESTS OF NEUTRAL POPULATION

Tajima's D , based on the more rapidly evolving control region, was 2.1 ($n = 32$), which is significant based on the 95% confidence intervals given in Tajima (1989a). A significant value indicates that either the population is not in mutation-drift equilibrium or that selection has occurred. However, Tajima (1989b) suggested comparing separate gene regions (coding vs. noncoding) in order to prevent rejecting the neutral hypothesis falsely. Tajima's D for the 12S gene was -1.0 , which was not significant. The fact that D -values were opposite in sign suggests that inferences based on so few sites (two variable sites in each gene) are unreliable because each site has a very large effect. A mismatch distribution (Rogers 1995) can also be used to test for a population bottleneck followed by a range expansion; again however, conflicting results indicate that the extremely low number of variable sites makes the validity of the results questionable. The simulated expansion model and the actual data for the control region differed significantly ($P < 0.05$), whereas no evidence was found to reject a population expansion with the 12S gene ($P = 0.4$). However, with such small genetic variability as found in Andean Condors, distinguishing between scenarios is difficult.

DISCUSSION

The results of this study show that genetic variability in mitochondrial genes of Andean Con-

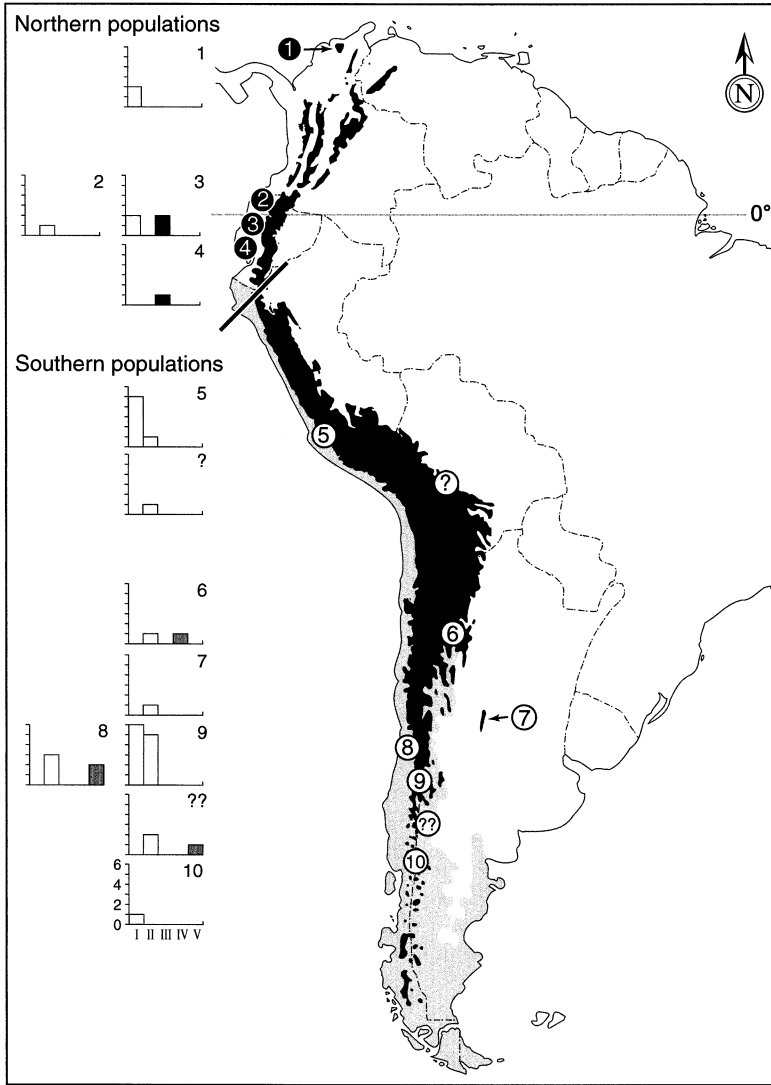


FIGURE 1. Map of historical range of Andean Condors based on records of sightings (Fjeldså and Krabbe 1990) and suitable habitat: black areas are elevations over 2000 m, gray areas are temperate grasslands. The Northern Peruvian Low (diagonal black bar) separates the páramo from the puna. Histograms represent the proportion of samples at each locality with a given haplotype. Haplotypes, based on variable sites at base-pair positions 817 and 851 (Domain II) and 1199 and 1318 (12S gene): I-CCTA, II-TTTA, III-CCTG, IV-CCCA, V-CTTA. Alleles unique to the area north and south of the Northern Peruvian Low are shown in black and gray respectively. Question marks denote sample localities that are uncertain, but near where indicated.

dors is extremely low. Low genetic variability in Andean Condors is particularly noteworthy given that samples were obtained from populations distributed over a large and physiographically heterogeneous area. In particular, we found no association between number of mitochondrial haplotypes and patterns of population scarcity

and heterogeneity (northern versus southern samples) or degree of isolation.

Our results for Andean Condors reinforce previous evidence for low genetic variability in large-bodied species. Genetic variability is thought to be lower in large predatory or scavenging birds as a result of the small effective

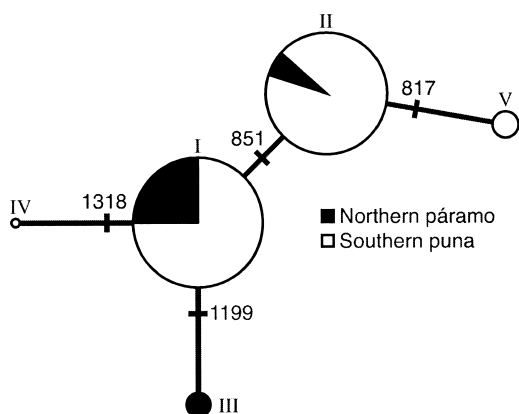


FIGURE 2. Minimum spanning network of the five Andean Condor haplotypes distributed over Domain II, Domain III, and 12S sequences. Pie chart diameter is proportional to the number of individuals with each haplotype. The proportions of individuals from the northern páramo and the southern puna are shown in black and white respectively. The positions of substitutions are numbered.

population size due to a high position in the food chain (Barrowclough and Gutiérrez 1990), large home-range size (Selander and Kaufman 1973), and relative scarcity. As scavengers in the Cathartidae (AOU 1998), Andean Condors exemplify these characteristics; moreover, they raise a single offspring in each brood, attempt to nest once every two years, and do not reach sexual maturity until eight years of age (Wallace and Temple 1988, Temple and Wallace 1989). This would result in a slow recovery from a population bottleneck because of low population numbers. A small effective population size alone could produce low variability through conventional population-genetic processes, such as non-selective loss of alleles by random genetic drift (Wright 1931, Crow and Kimura 1970). Further, new mutations would spread slowly through a sparsely distributed population. This would be enhanced by the linear range of the Andean Condor (Wright 1953).

Low genetic variability in megafauna also could result from several processes at the molecular level. Large body mass, and the associated lowering of metabolic rate, could slow the accumulation of new genetic variants by reducing the overall mutation rates (Martin and Palumbi 1993, Mindell et al. 1996, Bleiweiss 1998). Alternatively, mitochondrion-specific phenomena could reduce variability by one or more mechanisms.

First, strong selection to retain secondary structure in the control region could occur (Brown et al. 1986, Crocket and Desmarais 2000). Second, selection on any component of the mitochondrial genome could cause fixation of other components because the genes form a single linkage group (Baker and Marshall 1997). Third, unrecognized mitochondrial sequences translocated to the nucleus could have assumed evolutionary rates more typical of nuclear sequences (Sorenson and Quinn 1998). We are studying the possible contribution of these various mechanisms. Preliminary studies of secondary structure in the condor control region sequences are inconclusive. Nevertheless, whole-genome methods (fingerprinting: Negro and Torres 1999) and allozymes (Morizot et al. 1985, Barrowclough and Gutiérrez 1990, Negro and Hiraldo 1994) also reveal low genetic variability in predatory or scavenging birds, suggesting that the pattern of low variability occurs as well in nuclear genes and therefore its causes may transcend characteristics of specific genomic reasons.

Although methods are available for identifying historical bottlenecks, which are often cited as the main reason for low variability in other species, the condor data yield conflicting results, likely due to the few sites available for analysis. Data from other genes are needed; however, it may be that many of the factors suggested above affect the level of variability, and it will be difficult to determine exact causes of low variability.

Despite the low variability of the control region found throughout the Andean Condor's range, some geographic structure was detected. A significant difference in the frequencies of each haplotype was found between northern and southern populations, indicating that geography, or philopatry and breeding structure is affecting gene distributions. These data are provisional such that additional markers or observations of condor breeding structure are needed to clarify population structure and conservation management units.

GENETIC VARIABILITY AND CONSERVATION

Evidence that widespread species under no immediate danger of extinction exhibit low levels of genetic variability has important conservation implications. Most genetic studies of megafauna are done only after the populations have been reduced in size and abundance. Results with Andean Condors suggest that levels of genetic var-

TABLE 3. Levels of control-region variability in condors and other birds.

Species	No. of base pairs	<i>n</i>	No. of variable sites	Haplotype numbers			Nucleotide diversity ($\pi \pm$ SE)	Source
				Observed	Expected ^a	Ratio		
Species with low diversity								
Andean Condor	501 ^b	32	2	3	4.9	0.6	0.0020 \pm 0.0016	This study
Whooping Crane (postbottleneck)	317 ^c	24	4	4	4.8	0.8	0.0045 \pm 0.0032	Glenn et al. 1999
California Spotted Owl	1105 ^c	20	6	5	4.5	1.1	0.0006 \pm 0.0005	Barrowclough et al. 1999
Outbred species								
Northern Spotted Owl	1105 ^c	20	30	11	4.5	2.4	0.0050 \pm 0.0027	Barrowclough et al. 1999
Mexican Spotted Owl	1105 ^c	33	35	22	5.3	4.2	0.0055 \pm 0.0029	Barrowclough et al. 1999
Dunlin	608 ^c	155	43	39	7.4	5.3	0.0160 \pm 0.0080	Wenink et al. 1996
Willow Tit	1207 ^d	25	52	25	4.8	5.2	0.0053 ^e	Kvist et al. 1998
Great Reed Warbler	494 ^f	106	29	33	6.9	4.8	0.0071 \pm 0.0004	Bensch and Hasselquist 1999

^a Expected number of haplotypes if the haplotype diversity is the value observed for Andean Condors (0.595).

^b Domains II and III.

^c Domains I and II.

^d Domains I–III.

^e Standard error not reported.

^f Domain III.

iability may be low in large animals even without any known restrictions to their natural population sizes. This may provide an important context for the interpretation of genetic variation in threatened forms such as the California Condor. Although also once widespread (Steadman and Miller 1987), California Condors declined during the last few centuries to a low of five wild individuals in 1987 (Snyder and Snyder 2000). The recent genetic studies of this species (Corbin and Nice 1988, Geyer et al. 1993, Miller 1995) were necessarily based on the captive population, and therefore could not assess how much variation might have existed in the original wild ancestors. Comparisons of the amount of genetic variation present in threatened populations to that which existed either prior to the decline (e.g., among museum samples), or in related, nonthreatened species, should provide valuable insights into the relationship between genetic variability, body size, and rarity.

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APPENDIX. Sources and localities of Andean Condor DNA. "Source" includes the organization, original collector (if known), and accession number.

ID	Locality	Source
Haplotype I		
1	Coastal Peru	University of Wisconsin Zoological Museum, J. McGahan, 1970
3	Pisco, Peru	University of Wisconsin Zoological Museum, J. McGahan, 20284
5	Mendoza, Argentina	Jardín Zoológica de la Ciudad de Buenos Aires, RNCA 46
8	Mendoza, Argentina	Jardín Zoológica de la Ciudad de Buenos Aires, RNCA 43
9	Mendoza, Argentina	Jardín Zoológica de la Ciudad de La Plata, RNCA 45
14	Mendoza, Argentina	Jardín Zoológica de la Ciudad de Buenos Aires, RNCA 44
16	Mendoza, Argentina	Fundación Zoológica de Hurlingham, RNCA 32
20	Mendoza, Argentina	Jardín Zoológica de la Ciudad de Buenos Aires, RNCA 42
25	Antisana, Ecuador	Museo Ecuatoriano de Ciencias Naturales, 1977
27	Antisana, Ecuador	Fundación Antisana 1999
30	Mamancanaca, Colombia	National Museum of Natural History, M. A. Carriker, 386704
31	Mamancanaca, Colombia	National Museum of Natural History, M. A. Carriker, 386701
39	Coastal Peru	University of Wisconsin Zoological Museum, J. McGahan, 1970
41	Ica Department, Peru	Natural History Museum of Los Angeles, G. Ashton, 50061
44	Viguata, Peru	Academy of Natural Sciences, M. A. Carriker, Jr. 108252
47	Río Negro, Argentina	Natural History Museum of Los Angeles, A. Kovacs 56758
Haplotype II		
6	Mendoza, Argentina	Jardín Zoológica de la Ciudad de Buenos Aires, RNCA 20
10	Córdoba, Argentina	Jardín Zoológica de Córdoba, RNCA 21
11	Mendoza, Argentina	Jardín Zoológica de la Ciudad de Buenos Aires, RNCA 31
12	Catamarca, Argentina	Jardín Zoológica de Córdoba, RNCA 5
13	Mendoza, Argentina	Fundación Zoológica de Hurlingham, RNCA 33
15	Mendoza, Argentina	Jardín Zoológica de la Ciudad de La Plata, RNCA 1
18	Mendoza, Argentina	Jardín Zoológica de la Ciudad de Buenos Aires, RNCA 30
23	El Quiche, Ecuador	Hacienda Zuleta, F. Koester and F. Polanco
34	32°49', 34°20', Chile	Eduardo Pavez, JF1, Unión de Ornitólogos de Chile
35	32°49', 34°20', Chile	Eduardo Pavez, AF2, Unión de Ornitólogos de Chile
36	32°49', 34°20', Chile	Eduardo Pavez, AM3, Unión de Ornitólogos de Chile
45	Bolivia	Academy of Natural Sciences, M. A. Carriker, Jr., 167624
48	Argentina	Los Angeles Zoo, Chia
49	Argentina	Los Angeles Zoo, Bochica
Haplotype III		
22	Cuinca, Ecuador	Hacienda Zuleta, F. Koester, F. Polanco
24	Antisana, Ecuador	Museo Ecuatoriano de Ciencias Naturales, 1977
26	Pichincha, Ecuador	F. Sornoza, Fundación Jocotoco, private collection
Haplotype IV		
7	Catamarca, Argentina	Fundación Zoológica de Hurlingham, RNCA 6
Haplotype V		
17	Argentina	Jardín Zoológica de la Ciudad de Buenos Aires, RNCA 28
37	32°49', 34°20', Chile	Eduardo Pavez, AF4, Unión de Ornitólogos de Chile
38	32°49', 34°20', Chile	Eduardo Pavez, AM5, Unión de Ornitólogos de Chile