

to have low toxicity (manufacturer's Materials Safety Data Sheet). The powder has no detectable odor to humans. The trail to the first overnight brood site can be followed up to three days after marking and is not affected by light rain or dew. If the brood is to be recaptured, however, the trail must be followed the night of the original capture, given that the trail away from the overnight brood site tends to be less obvious and harder to follow.

There are several potential drawbacks to using the fluorescent powder. This method does not permit actual location-time distributions or speed of movement, and probably is ineffective with flying members of broods. Monitoring a broods movements over several days or weeks is not possible without reapplying powder. Finally, powder may make chicks vulnerable to predation by altering their cryptic coloration; however, restricting powder to the ventral area minimizes its visibility. Despite these disadvantages, powder tracking has potential for tracing movements of a variety of precocial, terrestrial bird chicks, including quail and pheasants (Phasianinae), grouse (Tetraoninae), and Wild Turkeys (*Meleagris gallopavo*).

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Lack of Restriction-site Variation in Mitochondrial-DNA Control Region of Whooping Cranes (*Grus americana*)

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In 1941 the number of living Whooping Cranes (*Grus americana*) dwindled to just 15 individuals (Binkley and Miller 1983). However, as a result of conser-

vation efforts over the past 50 years, there are presently 164 birds in the wild and another 159 in captivity (C. Mirande pers comm.). This recovery is dramatic because grune cranes are long-generation-time species (12 years) with low annual fecundity (rarely more than one fledgeling per year). Despite captive breeding and other conservation programs, concerns about Whooping Crane survival persist. Not least of

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TABLE 1. Founder composite nesting areas (CNAs) of Whooping Cranes and their captive-born representatives used in this study. Feather samples shown in parentheses.

CNA ^a	Observation period	Status	Captive chicks ^b (birth year/ SPARKS no.)	Voucher location ^c	Reference
K-1	1967-1988	Active	1968/1031	ICF	Kuyt (1987)
K-2	1967-1990	Active	1968/1027	ICF	Snowbank and Mirande (unpubl. data)
K-3	1969-1990	Active	1974/1062	NMNS	Kuyt (1981a)
K-5	1967-1984	Active	(1969/1042)	PESC	Snowbank and Mirande (unpubl. data)
K-6	1967-1984	Active	1968/1032	ICF	Kuyt (pers. comm.)
K-7	1969-1984	Extinct	Not available	—	Kuyt (1981b)
K-U	1968-1970	Active	1969/1041	ICF	Kuyt (1981b)
S-1	1966-1977	Active	1984/1128	ICF	Kuyt (1981b)
S-2	1967-1977	Active	(1967/1020)	PESC	Kuyt (1981b)
S-3	1967-1978	Extinct	Not available	—	Kuyt (1981b)
S-4	1967-1984	Active	Not available	—	Kuyt (pers. comm.)
S-5	1968-1980	Extinct	(1968/1030)	NMNS	Kuyt (1981b)
S-6	1966-1976	Extinct	Not available	—	Kuyt (1981b)

^a Names of CNAs derived from rivers (Klewi and Sass) closest to nests and order in which nests were mapped by Canadian Wildlife Service.

^b SPARKS numbers those employed by Snowbank and Mirande (1991a, b) using Single Population Analysis and Record Keeping System (ISIS 1994).

^c Institution abbreviations: ICF (International Crane Foundation, Baraboo, Wisconsin, USA); NMNS (National Museum of Natural Science, Ottawa, Canada); PESC (Patuxent Environmental Science Center, Laurel, Maryland, USA).

these is the genetic legacy of the 1941 population bottleneck, including such standard conservation genetics problems as inbreeding effects and the loss of genetic polymorphism (Hendrick and Miller 1992).

Dessauer et al. (1992) examined electrophoretic variation at 24 presumptive allozyme loci in a sample of 15 wild Whooping Cranes. The level of heterozygosity they reported ($H = 0.048$) is not particularly low. Indeed, it is considerably higher than values reported for other endangered bird populations (e.g. $H = 0$ for 23 loci in *Strix occidentalis* from Oregon and California; Barrowclough and Gutiérrez 1990), and not much less than the average for many avian species ($H = 0.053$; Barrowclough 1983). Longmire et al. (1992) found that Whooping Cranes showed noticeably less polymorphism than other birds at a minisatellite locus homologous to a portion of the M13 bacteriophage genome. Nevertheless, sufficient variation existed at this locus for establishing paternity in six of seven cases. These studies suggest that, despite a recent bottleneck, modern Whooping Cranes are not genetically impoverished relative to other bird species. If true, this finding would ameliorate concerns that unavoidable inbreeding is actively mitigating against Whooping Crane recovery.

We assayed mitochondrial-DNA (mtDNA) variation among modern Whooping Cranes to determine how many distinct mtDNA haplotypes survived the 1941 bottleneck. Because of its haploid nature and maternal transmission, mtDNA experiences an effective population size just one-quarter of that for nuclear loci (Avise et al. 1984). This reduction in effective size translates into a shorter fixation time for

neutral haplotypes, making mtDNA polymorphism particularly sensitive to population bottlenecks. Rather than study the entire molecule, we focused on the control ("D-loop") region that many studies suggest is among the most variable mtDNA regions. Because all mtDNA loci are completely linked and nonrecombining, study of a single locus does not entail loss of accuracy, and restricting attention to a variable region enhances our ability to detect polymorphism. Furthermore, maternal transmission allows us to sample only direct descendants of the 1941 females. Such individuals, as described below, can be identified from genealogies and nest-site surveys.

Methods.—Aerial surveys of Whooping Crane nests in Wood Buffalo National Park (Northwest Territories, Canada) have been conducted each spring and autumn since 1954 (Novakowski 1966). In these surveys, the territories of each breeding pair have been carefully mapped. Cranes mate for life and show a high degree of philopatry and nest-site fidelity (Kuyt and Gossen 1987). The entire territory occupied by a single breeding pair over a succession of years is described as a "composite nesting area" or CNA (Kuyt 1981b). We compiled a list of CNAs established prior to 1970 from maps developed by Novakowski (1966), Kuyt (1976), and Kuyt and Gossen (1987). These 13 "founder CNAs" (Table 1) represent the territories of all possible surviving female descendants of the bottleneck population. Thus, our survey would not assay matrilineal lines that disappeared between 1941 and 1970. Four of the 13 founder CNA pairs have died since 1970, though some left offspring in the captive flock. Representative descendants of each founder CNA were

chosen by cross-referencing nest-site survey data with the Whooping Crane genealogy of S. Snowbank and C. Mirande (unpubl. report 1991). Blood or feather samples were obtained from nine cranes representing all but one of the active CNAs (Table 1).

DNA was extracted from blood samples using standard methods of cell lysis, organic extraction, proteinase digestion, and ethanol precipitation (Sambrook et al. 1989). Feather-DNA extraction followed the protocol of Leeton et al. (1992). For blood samples, a fragment of approximately 1,200 nucleotide base pairs (bp), including the *D*-loop and glutamic acid transfer-RNA (tRNA^{Glu}) regions, was targeted for amplification via the polymerase chain reaction (PCR; Sambrook et al. 1989). Primer sites flanking the target sequence were located in the ND6 (primer L16707) and tRNA^{Phe} (primer H1247) loci. The H1247 primer sequence was supplied by T. Quinn (pers. comm.); the sequence for L16707 is 5'-GCATAAAATAAGT-CATCAGA-3'. For feather samples, a fragment containing approximately 750 bp of the 3' end of the *D*-loop was amplified with primers L543 (T. Quinn pers. comm.) and H1247. PCR reactions were performed in a 100 μ l volume with 2 mM MgSO₄, 1 μ mol primers, 0.2 mM dNTPs, 1 \times Vent reaction buffer, and 2 units of Vent (*exo*⁻) DNA polymerase (New England Biolabs). Thermal-cycle parameters were as follows: denature (94°C, 1 min), anneal (56–58°C, 1 min), extend (70°C, 3 min); 30 cycles per reaction. PCR products were electrophoresed through a 1% agarose gel and onto a DEAE membrane (Shleicher and Schull) soaked in 10 mM EDTA and 0.5 M NaOH. Purified DNA was eluted from the membrane in a high salt buffer (1 M NaCl, 0.1 mM EDTA, and 20 mM Tris), extracted with water-saturated *n*-butanol, precipitated with ethanol, and rehydrated in 30–50 μ l of distilled water (Nickrent 1994). PCR products were digested with each of 17 restriction endonucleases: four-cutters *Alu* I, *Dpn* II, *Hae* III, *Hha* I, *Hpa* I, *Mse* I, *Rsa* I, *Taq* I; five-cutters *Dde* I, *Hinf* I; six-cutters *Bam*H I, *Dra* I, *Eco* RI, *Hind* III, *Ssp* I, *Vsp* I, *Xho* I. Many of these enzymes were selected in part because their recognition sequences are AT-rich, as is the avian *D*-loop (Saccone et al. 1987, Desjardins and Morais 1990). Restriction digests were performed in 20 μ l volumes according to manufacturers' instructions. Digested PCR products were loaded into a 3% agarose gel, electrophoresed 2 h at 62V, and visualized by ethidium bromide staining. Restriction-fragment sizes were compared to a commercial standard (pGEM DNA markers, Promega) on each gel.

Results.—Four of the 17 restriction enzymes (*Bam*H I, *Eco* RI, *Ssp* I, and *Xho* I) did not cut the Whooping Crane *D*-loop fragments. Each of the remaining enzymes detected from 1 to 10 restriction sites for a total of 40 sites (252 bp assayed, roughly 20% of *D*-loop sequence). As expected, the enzyme with the shortest, AT-rich recognition sequence detected the largest number of sites (*Mse* I = TTAA, 10 sites). Despite the

large number of sites detected, restriction-fragment patterns were identical for each of the 10 cranes. This suggests that all Whooping Cranes whose ancestry traces through one of the nine founding CNAs assayed here possess a common haplotype.

Discussion.—Three plausible hypotheses can be constructed to explain the apparent lack of variation among Whooping Crane *D*-loop sequences. First, there may be multiple *D*-loop haplotypes, but with so few sequence differences that they could not be detected as RFLP variation with the 17 endonucleases employed here. Second, there may be multiple mtDNA haplotypes, all of which have identical *D*-loop sequences. Third, there may be only one mitochondrial haplotype remaining in the species.

Evaluation of the first hypothesis would require analysis of complete *D*-loop sequences. Although we lacked resources to complete this task, we did examine 72 to 280 bp of DNA sequence at the 3' terminus of the *D*-loop in six of the founder CNA representatives (data not shown; for sequencing protocols, see Krajewski and Fetzner 1994, Nickrent 1994). We again detected no variation among individuals. Wenink et al. (1994) documented average intraspecific *D*-loop divergences of 0.9% among five Ruddy Turnstones (*Arenaria interpres*) and 2% among three Dunlins (*Calidris alpina*). The most variable *D*-loop region in these shorebirds is the 3' terminal 243 bp, precisely the region we sequenced in Whooping Cranes. Thus, the available data suggest that, if multiple *D*-loop haplotypes exist in Whooping Cranes, the divergence among them is likely to be very small. This possibility awaits testing with complete sequences.

The second hypothesis suggests that sequence variation among mtDNA haplotypes exists outside of the *D*-loop region. Moum and Johansen (1992) indicated that apparent rates of sequence evolution in the ND6 gene of murres were high enough to make this locus useful for studies of intraspecific variation. This also is true in cranes (C. Krajewski and T. C. Wood unpubl. data). Therefore, we digested a 750-bp PCR product containing the entire ND6 sequence from each of the founding CNA representatives with 15 restriction endonucleases. Only six of these enzymes had recognition sequences in the ND6 region, and those six produced only two or three restriction fragments each. Again, however, there was no variation among individuals. In contrast, Wood and Krajewski (unpubl. data) detected nine distinct haplotypes in a sample of nine Sarus Cranes (*Grus antigone*) based on sequence-level variation in the cytochrome *b* and ND6 loci. Many of these haplotypes could be distinguished as RFLP variants using the restriction enzymes employed here.

We consider the third hypothesis most likely, that living Whooping Cranes have a single mtDNA haplotype. In 1956 there were an estimated six pairs of Whooping Cranes on nesting territories (Allen 1956). This places an upper limit (six) on the number of

surviving maternal lineages, and genealogical data (albeit incomplete prior to 1970) suggest that a more likely estimate is three or four (McNulty 1966, Captive Breeding Specialist Group unpubl. report 1991). These females would have had to represent distinct maternal lineages marked by mtDNA variants prior to the 1941 bottleneck to transmit multiple haplotypes to their post-1970 descendants. This scenario seems unlikely in light of the data presented here and the recent population history of Whooping Cranes.

Modern Whooping Cranes migrate annually from nesting grounds in Wood Buffalo National Park in the Northwest Territories of Canada to a wintering area at Aransas National Wildlife Refuge on the coast of Texas. Historically, however, the range of Whooping Cranes probably stretched from the Arctic to central Mexico, and from Utah to the Atlantic coast (U.S. Fish and Wildlife Service 1994). Estimates of presettlement population sizes vary from 500 to 5,000 (Allen 1956), although Binkly and Miller (1983) suggested that the largest pre-1900 population included at most 1,300 birds. By the late 1800s only two populations of Whooping Cranes remained, one at Wood Buffalo and a small, nonmigratory flock in southwestern Louisiana. The latter consisted of only 13 birds when it was effectively wiped out by a hurricane in 1940 (McNulty 1966, Gomez 1992). The size of the Wood Buffalo flock declined steadily throughout the early 1900s due to habitat loss and hunting pressure, reaching a low of 15 in 1941. The number of breeding females in the current wild Whooping Crane population is approximately 30% of the total population size (C. Mirande pers. comm.). Applying this conversion to the presettlement census estimates of Allen (1956) suggests an effective size of 150 to 1,500 females; the value for Binkly and Miller's (1983) estimate is 390 females. Thus, the 1941 bottleneck represents an approximately 20- to 200-fold reduction in the number of breeding females.

Wilson et al. (1985) noted that, after a severe but transient bottleneck, organelle DNA diversity may go to zero, whereas nuclear DNA diversity remains relatively high. In a prolonged bottleneck, however, polymorphism in both DNA types could be eliminated. Dinnerstein and McCracken (1990) examined both allozyme and mtDNA variation in the greater one-horned rhinoceros (*Rhinoceros unicornis*). Although the rhinoceroses have very low mtDNA divergences, their level of allozyme heterozygosity is high ($H = 0.099$), a pattern that Dinnerstein and McCracken (1990) attributed to a transient bottleneck. This finding parallels the situation in Whooping Cranes, and we suggest that similar historical demographic scenarios may apply to the two species.

In summary, Whooping Cranes do bear the genetic imprint of their near extinction in 1941. This event is manifested in currently low mtDNA diversity, but the relatively rapid recovery of the species due to intense conservation efforts has prevented a corre-

sponding loss of nuclear DNA variation. To date there have been no published or otherwise well-documented accounts of inbreeding effects in wild Whooping Cranes, although there is a high incidence of scoliosis and other spinal deformities in the captive flock, maladies that may be genetically based (C. Mirande pers. comm.).

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Female Bluethroats (*Luscinia s. svecica*) Regularly Visit Territories of Extrapair Males Before Egg Laying

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Recent evidence suggests that female birds play a more active role in sperm competition than traditionally recognized. Rather than passively awaiting male intruders, females may actively seek extrapair mates by moving outside their mate's territory (Kempnaers et al. 1992). Very little is known, however, on the movements of mated females before egg laying. We radio-tracked six female Bluethroats (*Luscinia s. svecica*) during the prelaying period to investigate whether they regularly move outside their mate's territory, a behavior that may allow assessment of and copulations with potential extrapair mates.

During the last decade, extrapair paternity has been demonstrated in an increasing number of bird species

(Smith 1984, Birkhead and Møller 1992). Traditionally, multiple matings in birds have been interpreted as the result of male efforts to increase their own fitness by pursuing a mixed reproductive strategy of caring for their own offspring and seeking extrapair copulations (EPCs; Trivers 1972). According to this view, EPCs result from competition between males for fertilizable females, whereas females are considered almost passive. Recent studies, however, suggest that females may have a much more active role in extrapair mating and sperm competition (e.g. Smith 1988, Montgomerie and Thornhill 1989, Kempnaers et al. 1992, Lifjeld and Robertson 1992, Wagner 1992, Lifjeld et al. 1994, Mills 1994, Sheldon 1994). For in-