

Population Fragmentation, Loss of Genetic Variation, and Reduced Fitness in Greater Prairie Chickens



*by Robb F. Leary
Montana Fish, Wildlife & Parks
Division of Biological Services
University of Montana
Missoula, Montana 59812*

Table of Contents

[CASE STUDY #2: Population Fragmentation, Loss of Genetic Variation, and Reduced Fitness in Greater Prairie Chickens](#)

[What is Population Fragmentation?](#)

[Breeding Patterns](#)

[Historical Distribution](#)

[Current Distribution](#)

[Genetic Drift's Impact](#)

[Research Results](#)

[Additional Studies](#)

[What Does It All Mean?](#)

[Literature Cited](#)

What is Population Fragmentation?

From a genetics perspective, *population fragmentation* is a major concern of conservation biology. It can potentially result in the establishment of a *genetic extinction vortex* (e.g. Gilpin and Soule 1986).

The hypothesized process operates as follows.

- Once continuously distributed or interconnected populations via gene flow become isolated due to some factor or factors such as habitat degradation.
- This in turn results in reduced demographic population size which coupled with reduced gene flow results in reduced *effective population size (N_e)*.
- Reduced N_e increases the amount of *genetic drift* and the rate at which *genetic variation* is lost from populations.
- Over a number of generations this reduced N_e and concomitant genetic drift can result in a significant reduction in the amount of genetic variability and an increase in the degree of relationship among individuals within populations.

The loss of *genetic variability* can begin compromising *population viability* further reducing population size by negatively influencing a variety of *fitness* attributes of individuals such as growth, disease resistance, survival, fertility, and development (e.g. Mitton and Grant 1984; Allendorf and Leary 1986; Palmer and Strobeck 1986; Zouros and Foltz 1987; Hedrick and Kalinowski 2000; Keller and Waller 2002; Borrell et al. 2004; Spielman et al. 2004).

The increased degree of relatedness among individuals also results in *inbreeding* which in turn can result in *inbreeding depression* further compromising fitness attributes and population viability (e.g. Hedrick and Kalinowski 2000; Keller and Waller 2002). Thus, demographic population size may decrease further resulting in even lower N_e and increased inbreeding exacerbating the negative consequences of these factors. This continued cycle, therefore, if left unabated has the potential by itself to cycle populations into extinction (e.g. Spielman et al. 2004).

Greater prairie chickens *Tympanuchus cupido* probably represent a good example of this phenomenon.

Breeding Patterns

Greater prairie chickens possess a lek mating system. That is, dominant males establish breeding areas and attract females via "booming". Thus, in any one breeding season only about ten percent of the males may successfully reproduce (e.g. Johnson et al. 2004) meaning that N_e is substantially less than the demographic population size.

Greater prairie chickens, therefore, may be especially susceptible to the potential adverse genetic effects of population fragmentation and the establishment of a genetic extinction vortex.



Historical Distribution

Historically, the greater prairie chicken was distributed throughout the tall grass prairie of central North America (e.g. Westemeier et al. 1998; Johnson et al. 2003; Figure 1).



Figure 1. Approximate historic (black line) and current distribution (black areas) of greater prairie chickens. IL=Illinois, KS=Kansas, MN=Minnesota, MO=Missouri, NE=Nebraska, WI=Wisconsin.

Before human modification of the habitat, it is believed that tens of millions of birds existed throughout the prairie. For example, it is estimated that within Illinois alone during the 1860's there were several million birds (Bouzat et al. 1998a, b; Westemeier et al. 1998). Furthermore, it appears that substantial gene flow existed throughout the prairie (Johnson et al. 2003).

Current Distribution

Due to human mediated loss of habitat, greater prairie chickens are no longer continuously distributed throughout the central plains. Rather, they exist in isolated fragmented groups of birds mainly being centered in Illinois, Kansas, Minnesota, Missouri, Nebraska, and Wisconsin (Figure 1). By the mid-1990's and later, the demographic population sizes in the Kansas and Nebraska groups were generally still robust (Table 1). In Minnesota, Missouri, and Wisconsin, they were low but, not exceptionally so (Table 1). In Illinois, however, the demographic population size was critically low (Table 1).

Table 1

Estimated demographic numbers of greater prairie chickens in six remaining isolated groups.

Group	Estimated Size	References
Illinois	<50	1
Kansas	>100,000	1,3
Minnesota	2,000-4,000	1,3
Missouri	1,000	3
Nebraska	>100,000	1,3
Wisconsin	1,200-1,500	2,3

References: 1=Bouzat et al. 1998a, 2=Bellinger et al. 2003, 3=Johnson et al. 2003.

Greater prairie chickens once inhabited about every county in Wisconsin (Bellinger et al. 2003). By 1930, however, it was estimated that only about 55,000 birds inhabited the state. In 1950, only about 2,500 birds remained in four isolated areas in the center of the state and by 1960 these birds declined in abundance to about half this size (Bellinger et al. 2003; Figure 2). Since this time the number of birds has fluctuated around this level. It is estimated that in this area greater prairie chickens have a generation time of about two years. Thus, these birds have experienced relatively low N_e for about 20-25 generations.



Figure 2. Current distribution of greater prairie chickens in central Wisconsin. From Johnson et al. (2004).

Johnson et al. (2003) used data from six *microsatellite loci* and *sequences* from 384 *bp* of *mtDNA* to compare levels of *genetic variation* and amounts of genetic divergence among birds from the four remaining groups in Wisconsin and ones collected from comparably sized areas in Kansas, Minnesota, Missouri, and Nebraska. At the microsatellite loci, *average expected heterozygosity* and *average number of alleles per locus* were used as estimates of amounts of genetic variation. Haplotype diversity was used to estimate mtDNA diversity. F_{ST} was used to examine amounts of genetic diversity between pairs of samples.

Considering all the Wisconsin birds as one group, they had the lowest average expected *heterozygosity* and haplotype diversity compared to the other groups and only the Missouri birds had a lower average number of alleles per locus (Table 2).

When the Wisconsin birds were treated as four separate groups, all three estimates of the amount of genetic variation in them were lower than in any of the other groups (Table 2).

Table 2					
Average expected heterozygosity (H_e) and average number of alleles per locus (A) at six microsatellite loci and haplotype diversity (h) for 384 bp of mtDNA in greater prairie chickens collected from Kansas, Minnesota, Missouri, Nebraska, and the four remaining Wisconsin groups. N=sample size. From Johnson et al. (2003).					
Group	N	H_e	A	N	h
Kansas	47	0.763	10.3	20	0.858
Minnesota	45	0.729	9.5	20	0.840
Missouri	20	0.709	7.7	20	0.866
Nebraska	48	0.731	10.5	20	0.968
Wisconsin (combined)	181	0.595	8.5	80	0.641
Wisconsin Groups					
Mead	32	0.598	6.3	20	0.484
Paul Olson	33	0.597	5.1	20	0.679
Buena Vista	87	0.560	7.0	20	0.511
Leola	29	0.560	6.2	20	0.784

Genetic Drift's Impact

Genetic drift is expected to not only result in reduced genetic variation but, also to result in increased genetic divergence among populations. Using either microsatellite loci or mtDNA, Johnson et al. (2003) found there was as much or more genetic divergence among the four Wisconsin groups as there was when birds from other states were compared (Table 3). When birds from Wisconsin were compared to those from the other states, the Wisconsin birds were by far the most divergent (Table 3). Overall, therefore, these data strongly suggest that the Wisconsin birds have experienced significant genetic drift resulting in reduced genetic variation and increased divergence.

Table 3			
Mean and range (in parentheses) of F_{ST} for microsatellite and mtDNA when pairwise comparisons are performed among the four Wisconsin groups (Wisconsin) of greater prairie chickens, between birds from other states besides Wisconsin (others), and pairwise comparisons between the four Wisconsin groups and birds from other states (Wisconsin vs. others). From Johnson et al. (2003).			
Comparison	Mean and range of F_{ST}		
	Microsatellites		mtDNA
Wisconsin	0.050 (0.017-0.087)		0.044 (-0.033-0.091)
Others	0.025 (0.008-0.050)		0.041 (-0.014-0.090)
Wisconsin vs. others	0.083 (0.057-0.099)		0.290 (0.123-0.441)

More direct evidence for significant genetic drift and a loss of genetic variation within Wisconsin greater prairie chickens was provided by Bellinger et al. (2003) and Johnson et al. (2004). Data were obtained from six microsatellite loci and sequences of 384 bp of mtDNA from historic (1951-1954) and contemporary (1998-2000) samples of birds from the four areas. Although average observed heterozygosity did not significantly differ between the historic and contemporary samples, average number of alleles per locus and haplotype diversity were significantly lower in the contemporary compared to the historic samples (Table 4).

Table 4					
Average observed heterozygosity (H_o) and average number of alleles per locus (A) at six microsatellite loci and mtDNA haplotype diversity (h) in historic and contemporary samples of greater prairie chickens collected from four areas in Wisconsin. N =sample size. From Johnson et al. (2004).					
Sample	N	H_o	A	N	h
Mead-historic	29	0.71	8.7	18	0.841
contemporary	32	0.61	6.3	20	0.484
Paul Olson-historic	25	0.67	8.3	19	0.860
contemporary	33	0.64	5.1	20	0.679
Beuna Vista-historic	42	0.71	9.2	19	0.889
contemporary	87	0.56	7.0	20	0.511
Leola-historic	29	0.61	8.5	17	0.890
contemporary	29	0.57	6.2	20	0.784

There was little genetic divergence at both microsatellite loci and mtDNA among the four historic samples (Table 5). In contrast, there was appreciable divergence among the contemporary samples and between the contemporary and historic samples (Table 5).

Table 5		
Mean and range (in parentheses) of F_{ST} for microsatellite and mtDNA data for pairwise comparisons within historic and contemporary samples of greater prairie chickens and between historic and contemporary samples (between) collected from four areas in Wisconsin. From Johnson et al. (2004).		
Samples	Mean and range of F_{ST}	
	Microsatellite	mtDNA
Historic	0.013 (0.004-0.026)	0.000 (-0.018-0.018)
Contemporary	0.038 (0.017-0.087)	0.044 (-0.033-0.091)
Between	0.069 (0.038-0.119)	0.243 (0.023-0.470)

Finally, estimates of N_e based on the allele frequency differences at microsatellite loci observed between the historic and contemporary samples were all low and much

lower than the estimated demographic population sizes (Table 6).

Table 6			
Estimated demographic population size and effective population size (N_e) for greater prairie chickens collected from four locations in Wisconsin. N_e estimates are based on allele frequency differences at six microsatellite loci observed between historic and contemporary samples. From Johnson et al. (2004).			
Sample	Demographic Size		N_e
Mead	174		19
Paul Olson	181		15
Buena Vista	432		25
Leola	99		16

Research Results

The above results directly indicate that Wisconsin greater prairie chickens have lost significant levels of genetic variation due to population fragmentation and subsequent genetic drift. Interestingly, such effects were not noticeable in the Minnesota and Missouri birds although the total number of birds in these states was comparable to that observed in Wisconsin (Table 1).



This difference probably reflects that within Minnesota and Missouri the birds occupy continuous habitat (Johnson et al. 2003) while in Wisconsin they are further fragmented into four isolated groups. Thus, N_e is likely to have been substantially larger in Minnesota and Missouri than in Wisconsin. From a genetics perspective, therefore, this observation attests to the conservation value of maintaining relatively large continuous patches of suitable habitat.

Additional Studies

Although the Wisconsin birds have lost significant genetic diversity, based on limited data this does not appear at this time to have negatively affected fitness attributes. Prior to 1950, hatching success fluctuated between 90 and 95% and in the late 1990's it was estimated to be 89% (Bellinger et al. 2003). Data from Illinois greater prairie chickens which will be subsequently presented, however, indicate that a severe reduction in N_e over time can have adverse fitness consequences. Thus, continued loss of genetic variation from Wisconsin greater prairie chickens may eventually begin compromising population viability. It has been suggested, therefore, that in order to better conserve Wisconsin greater prairie chickens that N_e be increased by moving birds among areas and possibly introducing them from other states (Johnson et al. 2003, 2004).

In Illinois, greater prairie chickens historically occupied greater than 60% of the state (Westemeier et al. 1998; Figure 3). The total number of birds in Illinois had declined from millions to an estimated 25,000 in 1933, to 2,000 in 1962, to 500 in 1972, to 76 in 1990, and to less than 50 in 1993 (Bouzat et al. 1998b; Westemeier et al. 1998). Now the birds are restricted to only two counties (Figure 3).

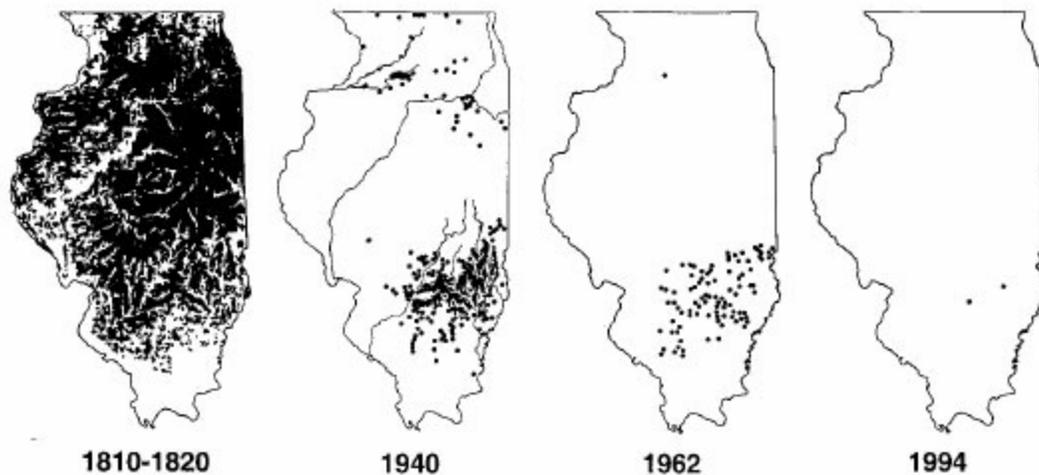


Figure 3. Distribution of greater prairie chickens in Illinois during different time periods. From Westemeier et al. (1998).

In Jasper County, the number of males on booming grounds declined from 84 in 1963 to about 40 in the mid-1960's (Westemeier et al. 1998; Figure 4). In the mid-1960's, habitat improvement measures began and by 1972 the number of males had increased to an estimated 206 (Westemeier et al. 1998; Figure 4). Subsequently, however, hatching success began to decline from over 90% in the early 1960's to less than 80%

in the early 1990's while in larger populations outside Illinois it averaged over 94% during this time period (Westemeier et al. 1998; Figure 4). Despite increased efforts at habitat improvement during this time, concomitant with this reduced hatching success the number of birds progressively declined such that in 1994 only five or six males remained in the population (Figure 4).

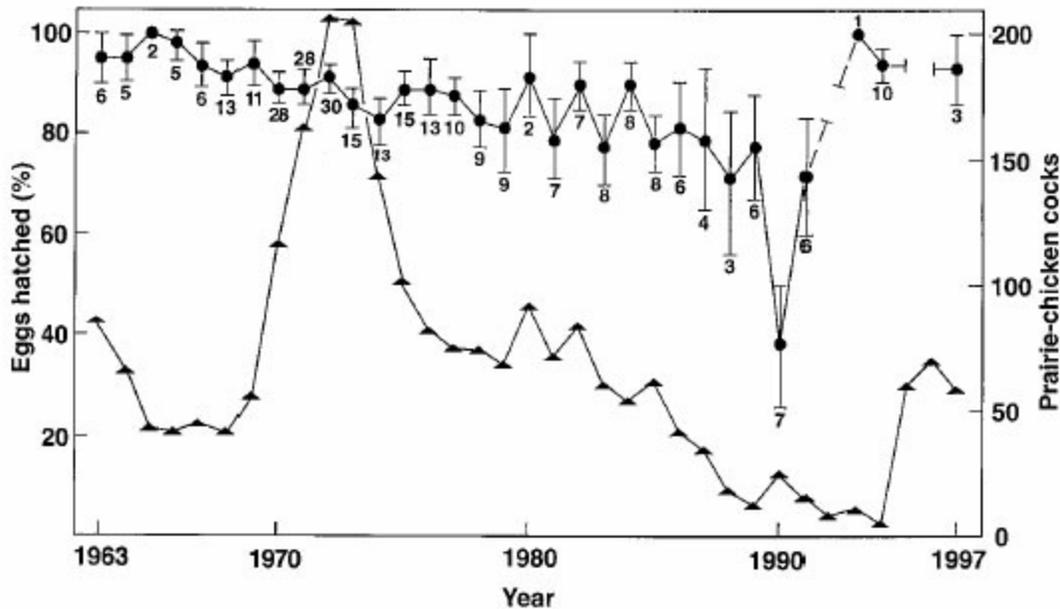


Figure 4. Estimated number of male prairie chickens (triangles) and hatching success of eggs (circles, numbers represent number of nests from which data were obtained) in Jasper County, Illinois from 1963-1997. Birds (N=271) from Kansas, Minnesota, and Nebraska were introduced from 1992-1996. Note the subsequent increase in the number of males and hatching success. From Westemeier et al. (1998).

Bouzat et al. (1998a, b) obtained data from six microsatellite loci from birds collected from the Jasper County Illinois population from 1974-1993 (contemporary) and 15 museum specimens collected during the 1930's and early 1960's (historic) as well as birds from Kansas, Minnesota and Nebraska collected from 1992-1994. Although average observed heterozygosity did not significantly differ among the contemporary Illinois, Kansas, Minnesota, and Nebraska samples, the contemporary Illinois birds had the lowest estimate and also had a significantly lower average number of alleles per locus than any of the other samples (Table 7).

Table 7					
Average observed heterozygosity (H_o) and average number of alleles per locus (A) at six microsatellite loci in samples of historic and contemporary greater prairie chickens collected from Jasper County, Illinois and contemporary birds collected from Kansas, Minnesota, and Nebraska. N=sample size. NR=data not reported. From Bouzat et al. (1998a, b).					
Sample	N		H_o		A
Kansas	37		0.597		5.83
Minnesota	38		0.654		5.33
Nebraska	20		0.626		5.83
Illinois (historic)	15		NR		5.12
Illinois (contemporary)	32		0.571		3.67

Furthermore, little genetic divergence was observed among the Kansas, Minnesota, and Nebraska birds but, the contemporary Illinois birds were quite divergent from these others. These data, therefore, strongly indicate that the Illinois birds have lost substantial amounts of genetic variation due to population fragmentation and genetic drift.

What Does It All Mean?

The question now is whether or not the reduction in amounts of genetic variation and the progressive reduction in hatching success and population size from the early 1970's through the early 1990's were causally related. There are three pieces of evidence that suggest a causal relationship.



First, the reduction in hatching success was not observed in Kansas, Minnesota, Nebraska, and Wisconsin birds during this time frame ruling out large scale environmental factors as a potential cause.

In Illinois, May weather conditions are a major factor influencing hatching success with excessive rainfall and flooding or too little rain resulting in poor success (Westemeier et al. 1998). During much of the 1970's and 1980's, rainfall was generally favorable for hatching success suggesting that local environmental conditions also were probably not responsible for the observed trends (Westemeier et al. 1998).

Finally, between 1992 and 1996 144 female and 127 male greater prairie chickens from Kansas, Minnesota, and Nebraska were introduced into Jasper County (Westemeier et al. 1998). Hatching success in 14 nests observed in 1993, 1994, and 1997 increased from an average of 76% in the previous decade to an average of 94% (Westemeier et al. 1998; Figure 4). In 1993 and 1994, three nests were laid by Minnesota females, five by Kansas females, and three by females of unknown origin. With the exception of one male definitely of Illinois origin, the origin of the other males that bred with these females was unknown. The origin of all the male and females that produced the nests sampled in 1997 was unknown but, it is strongly suspected that they were of mixed origin. During 1993, 1994, and 1997 May rainfall in Jasper County was 85, 49, and 91% of normal suggesting that unusually favorable spring conditions were not responsible for the marked increase in hatching success.

Thus, overall these data suggest that greater prairie chickens in Illinois entered a

genetic extinction vortex during the early 1970's and that without the translocations performed in the 1990's that extinction was probably inevitable.

Literature Cited

- Allendorf, F. W., and R. F. Leary. 1986. Heterozygosity and fitness in natural populations of animals. Pages 57-76 in M. E. Soule, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Bellinger, M. R., J. A. Johnson, J. Toepfer, and P. Dunn. 2003. Loss of genetic variation in greater prairie chickens following a population bottleneck in Wisconsin, U.S.A. *Conservation Biology* 17:717-724.
- Borrell, Y. J., H. Pineda, I. McCarthy, E. Vazquez, J. A. Sanchez, and G. B. Lizana. 2004. Correlations between fitness and heterozygosity at allozyme and microsatellite loci in the Atlantic salmon, *Salmo salar* L. *Heredity* 92:585-593.
- Bouzat, J. L., H. H. Cheng, H. A. Lewin, R. L. Westemeier, J. D. Brawn, and K. N. Paige. 1998a. Genetic evaluation of a demographic bottleneck in the greater prairie chicken. *Conservation Biology* 12:836-843.
- Bouzat, J. L., H. A. Lewin, and K. N. Paige. 1998b. The ghost of genetic diversity past: historical DNA analysis of the greater prairie chicken. *The American Naturalist* 152:1-6.
- Gilpin, M. E., and M. E. Soule. 1986. Minimum viable populations: processes of species extinction. Pages 19-34 in M. E. Soule, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Hedrick, P. W., and S. T. Kalinowski. 2000. Inbreeding depression in conservation biology. *Annual Reviews in Ecology and Systematics* 31:139-162.
- Johnson, J. A., M. R. Bellinger, J. E. Toepfer, and P. Dunn. 2004. Temporal changes in allele frequencies and low effective population size in greater prairie-chickens. *Molecular Ecology* 13:2616-2630.
- Johnson, J. A., J. E. Toepfer, and P. O. Dunn. 2003. Contrasting patterns of mitochondrial and microsatellite population structure in fragmented populations of greater prairie-chickens. *Molecular Ecology* 12:3335-3347.
- Keller, L. F., and D. M. Waller. 2002. Inbreeding effects in wild populations. *Trends*

in *Ecology and Evolution* 17:230-241.

Mitton, J. B., and M. C. Grant. 1984. Associations among protein heterozygosity, growth rate, and developmental homeostasis. *Annual Review of Ecology and Systematics* 15:479-499.

Palmer, A. R., and C. Strobeck. 1986. Fluctuating asymmetry: measurement, analysis, and patterns. *Annual Review of Ecology and Systematics* 17:391-421.

Spielman, D., B. W. Brook, and R. Frankham. 2004. Most species are not driven to extinction before genetic factors impact them. *Proceedings National Academy of Sciences USA* 101:15261-15264.

Westemeier, R. L., J. D. Brawn, S. A. Simpson, T. L. Esker, R. W. Jansen, J. W. Walk, E. L. Kershner, J. L. Bouzat, and K. N. Paige. 1998. Tracking the long-term decline and recovery of an isolated population. *Science* 282:1695-1698.

Zouros, E., and D. W. Foltz. 1987. The use of allelic isozyme variation for the study of heterosis. *Isozymes: Current Topics in Biological and Medical Research* 13:1- 59.