Conservation Biology Research Grants Program
Nongame Wildlife Program
Division of Ecological Services
Minnesota Department of Natural Resources

# THE GENETIC AND DEMOGRAPHIC STATUS OF PEREGRINE FALCONS IN THE UPPER MIDWEST

S. M. MOEN AND H. B. TORDOFF 1993

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Report prepared for:

The United States Fish and Wildlife Service
and
The Minnesota Department of Natural Resources
Non-game Wildlife Program

September 1993

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## FORWARD

The following report on the genetic, demographic, and modeled status of Peregrine Falcons in the Midwest has been written in three chapters. We anticipate submitting each chapter for publication in a reviewed journal; we have formatted the chapters accordingly. Each chapter begins with an abstract and ends with a list of the references cited throughout the chapter. Appendices are compiled at the end of the report. Each report contains an IBM-compatible disk located in the pocket on the inside of the hack cover. The disk contains Appendix 3 (Laboratory Protocols), Appendix 5 and Appendix 6 (VORTEX input and output files) saved as ASCII text files for those readers who wish to pursue DNA fingerprinting and/or population modeling. Appendices 3,', 5, and 6 were not printed in an effort to conserve paper and lower printing costs.

Despite the intensity with which Peregrine Falcons have been monitored, bred, restored, and studied, there are still a multitude of questions that could be asked and answered abort their population biology. With the advent of molecular techniques allowing the exploration of the genome, the research questions can be broadened and deepened. Providing that political and environmental conditions permit the new peregrine population to thrive, its existence creates an unequaled opportunity for scientific research. Our intent, with this report, is to provide baseline data for future research of this undoubtedly unique population. This baseline data includes the genetic state of the new population as derived from DNA analyses and pedigree information. We present demographic parameters that are essential for forming basic population models. We then use population modeling to examine the probable future of the Peregrine Falcons in the Upper Midwest.

The opportunity to conduct this research would not have been possible without the foresight of Dr. Patrick Redig, the encouragement of Dr. Mark Fuller and Dr. William

Seegar, and the assistance of countless falconers, professional biologists, and peregrine enthusiasts. We are indebted to Ronald Moen, Jon Longmire, Dr. Douglas Foster, Dr. Kevin Guise, Dr. Nathan Flessness, and Dr. Ulysses Seal for speeding our progress and expanding our horizons. We are grateful for the financial support of the U. S. Fish &Wildlife Service through M. Fuller and W. S. Seegar of the U. S. Army, The Minnesota Department of Natural Resources Non-game Wildlife Program through R. Baker, the Big Game Club Special Projects Foundation, the Graduate School of the University of Minnesota, the Dayton Natural History Fund and the Wilke Natural History Fund of the Bell Museum of Natural History, University of Minnesota.

# CHAPTER 1

ANALYSIS OF PEDIGREES

AND

POTENTIAL FACTORS INFLUENCING THE SUCCESS

OF

PEREGRINE FALCONS

IN THE

UPPER MIDWEST

## ABSTRACT

Once more, Peregrine Falcons are breeding in the Upper Midwest after about three decades of absence and 11 years of successfully hacking birds into the wild. The success of the peregrine recovery effort in the Midwest can be tallied by the genetic condition of the new population as well as by counting pairs in the wild. Pedigree analyses indicate that the Peregrine Falcons breeding in Upper Midwest (including Winnipeg and St. Louis) are relatively related (mean kinship falls between 0.026 and 0.053) and are moderately inbred (inbreeding coefficient is no less than 0.014). The high average relatedness of the population suggests that the inbreeding coefficient will rise as the population moves from being supplemented with hacked birds to becoming self-sustaining.

The relative importance of genetic, demographic, and environmental conditions in driving the founding event of this new population is uncertain. Particular individuals and pairs have been more successful than expected at producing offspring that survives in the wild. This suggests a genetic component to survival. However, the survival of the nest-mate (not necessarily a sibling) also appears to positively influence the survival of a fledgling suggesting an environmental component to survival as well. The subspecific condition of an individual does not seem to influence its success since pure *F. p. anatum* birds survive at a similar rate to pure *F.p. pealei* individuals and the ratio of subspecies fledged and those breeding is similar. A fledgling's chance of survival does not appear to depend on whether it was wild produced or hacked.

Peregrine releases in the Upper Midwest are virtually over as of fall 1993. Terminating the peregrine release effort should not jeopardize the new population's genetic integrity since the availability of unique genetic information is limited in the captive population. Continued banding and intense monitoring of the new population is essential, however. We recommend continued banding and monitoring of the population at least until the dramatic genetic changes involved in the founding event are over; particularly, we suggest that the level of inbreeding and kinship be calculated annually. A similar pedigree investigation should be initiated for the Canadian release project. Peregrines released in the lower Midwest of Canada and the Upper Midwest of the United States inter-breed freely and similar genetic stock supports both release projects. Should further releases in the Midwest be necessary, we suggest using genetically diverse individuals, especially birds that are not inbred and that are unrelated to falcons breeding in the wild.

## INTRODUCTION

Capture propagation leading to the release of animals in the wild is a popular technique for augmenting, establishing, or re-establishing populations (Arabian Oryx, Nene, Puerto Rican Parrot, California Condor, Black-footed Ferret, etc.). Captive breeding programs and the subsequent success of re-established or newly established populations often necessitate at least three founding events. Founding events, or population bottlenecks, occur when a small number of individuals generate a larger descendant population (Temple & Cade 1986). One founding event occurs when animals are brought in from the wild to establish a captive population. A second happens when a subset of their descendants are released back into the wild. A third takes place When a subset of the released animals survive and reproduce.

Depending on chance demographic events and the species in question, just one founding event followed by genetic drift can dramatically alter the gene pool available for evolutionary change (Wayne et al. 1991). The three founding events involved in many propagation-for-release efforts can greatly increase the probability that the resulting population will be genetically depauperate. After the founding event and in addition to genetic drift, differential reproduction in a small population can further increase its genetic identity.

One way to asses the loss of genetic diversity is through pedigree analyses. The focus of such analyses is on the genetic structure of a population with respect to its ancestry. Pedigree analyses usually assume that the genetic variation under study is selectively neutral and rely on known, knowable, or reasonably assumed or modeled ancestral linkages (Lacy et al. In Press). We used pedigree analysis as a method of assessing the genetic character of the new Peregrine Falcon (*Falco peregrinus*) population of the Upper Midwest.

During the last two decades well over 4000 captively bred Peregrine Falcons have been released in North America either to supplement depleted populations or reestablish extirpated ones (programs exist or existed in Eastern, Midwestern, Rocky Mountain region, and Western USA and in Canada)(Burnham & Cade, 1992). In 1976, the Minnesota Peregrine Group initiated a release program in an effort to reestablish peregrines in the Upper Midwest of the United States. This initial program was terminated after its second unsuccessful year but in 1982 the effort was resumed and has resulted in a new population of at least 33 breeding pairs in 1992 (Redig & Tordoff, 1992) and 51 in 1993.

From 1982 to 1992, at least 783 peregrines have fledged into the wild in the Upper Midwest of the United States and the Lower Midwest of Canada; a minimum of 152 of these birds were subsequently resighted a year or more after fledging (Appendix 1). Out of the peregrines resighted, 123 were identified by leg-band number of which 74 have bred. The wild fledglings they produced carry genetic material from at least five of 19 recognized subspecies but only about 50 out of about 75 wild-caught founders.

In this chapter, we analyze the genetic composition of the new population relative to the three founding events that led to its establishment. We evaluate the representation of true founders in the gene pool of peregrines that have survived at least a year in the wild. In an effort to determine what influences a peregrine's probability of surviving to adulthood, we compare the survival of released (hacked and fostered) to wild produced birds and hacked to peregrine-reared birds (wild produced and fostered). We also assess survival among subspecies and among sites. We conclude with the management and research implications of this study.

## METHODS

The major assumption underlying this work is that the peregrines identified in the wild adequately represent the true state of the wild population. Our calculations of survival to adulthood are based solely on birds that were identified by leg-band number and therefore certainly underestimate actual values. We use them in this chapter for comparative purposes only. Young that fledge in urban areas are more easily banded and might be more likely to be reidentified after fledging thus biasing our success estimates. We classify females that laid an egg in the wild and males that have sired a wild-laid egg as breeders. Birds that survived one year or more in the wild are classified as sighted.

Pedigree information was obtained from more than 50 breeders of falcons whose captive birds directly or indirectly contributed genes to the peregrines released in the Upper Midwest. Pedigree information was incorporated into "Single Population Analysis and Record Keeping System©" (SPARKS©). SPARKS is a database primarily used for managing international zoo populations and can be purchased from International Species Information System. For the genetic analysis, we exported data from SPARKS and arranged it for input into the complementary program GENES© written by R. Lacy (1992).

GENE calculated mean kinship and the expected heterozygosity retained for the specified sets of birds. Kinship measures the relatedness of two individuals by calculating the inbreeding coefficient of their hypothetical offspring. An individual's inbreeding coefficient is the probability that the alleles at a specific loci are identical by descent. Mean kinship is the average kinship value of all individuals. The program also summed, and averaged founder contributions to each living descendant.

We conducted analyses in two ways:

1) Gems descending from unknown ancestors were eliminated,

2) Unknown ancestors were treated as founders.

Eliminating unknown ancestors from the analysis produces a conservative but unbiased estimate of mean inbreeding and allelic diversity. An individual with one unknown parent is treated as half an animal (haploid) and similarly an animal with one unknown grandparent is treated as three quarters of an animal. Genetic parameters calculated for partial animals are based exclusively on genes that can be traced to true founders. Treating unknown ancestors as unique founders provides an upper limit for allelic diversity and a lower limit for inbreeding and kinship coefficients.

We ran GENES using the following comparisons:

1) Captive birds relative to founders brought into captivity,
2) Birds released prior to 1992 relative to founders brought into captivity,
3) Birds that lived at least one year in the wild relative to their ancestors (not every captive founder),
4) Post-hatch year birds alive during the 1992 breeding season relative to their ancestors (not every captive founder),
5) Breeding birds in 1992 relative to their ancestors (not every captive founder).

## RESULTS

### Genetic Status

The 531 peregrines released in the Upper Midwest of the United States from 1982 through 1991 (see Chapter 3) can be traced back to a minimum of 59 wild caught individuals from around the world (Fig. 1). A maximum of 128 founders have had an opportunity to contribute genetic material if we assume all birds with unknown ancestry are unrelated. This assumption is undoubtedly incorrect since most of the unknown ancestors come from only three breeding facilities. Furthermore, although pedigrees do not exist for the peregrines released before 1986 they are from the same breeding institutions as later releases. Most likely, there are between 70 and 80 true founders (unrelated ancestors brought in from the wild for captive breeding) with descendants released into the Upper Midwest.

The probability that homologous genes chosen at random from two individuals are identical by descent (mean kinship) increases from 0.035 to 0.053 between released falcons and those that have bred if unknown founders are eliminated from the calculation (Table 1). If the 59 true founders all had two different alleles for the same gene, between 41 and 50% of the original genetic diversity released into the Upper Midwest is theoretically lost in the breeding population. The calculation for founder equivalents indicates the same genetic parameters could result from founding the population with 10 to 19 equally represented birds, assuming no random loss of alleles (Table 1).

Figure 1. Map of the subspecific origins of the 59 known founders of the peregrines released in the Upper Midwest through 1991.

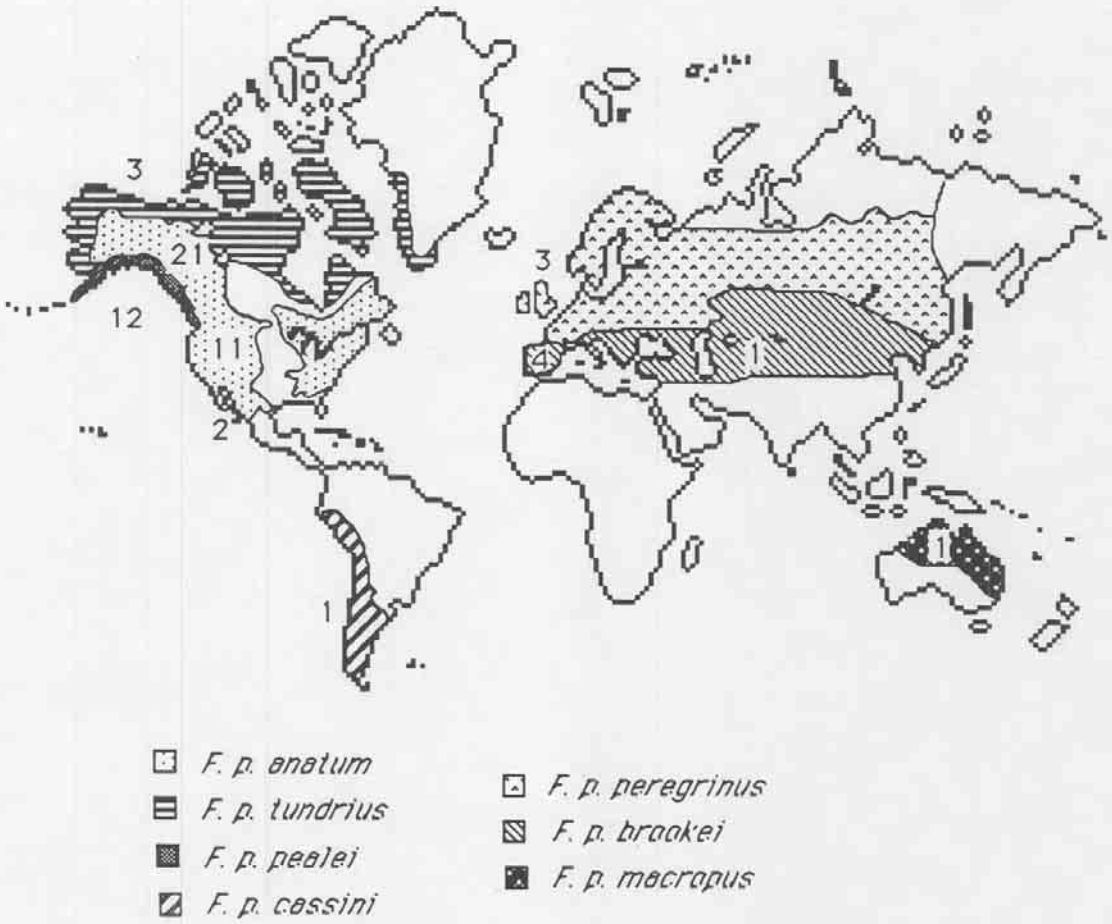


Table 1. Results of genetic analysis. Ranges were calculated by assuming that birds with unknown origins are founders and by eliminating birds with unknown origins. "Sighted" includes the released and wild produced birds identified at least one year after fledging into the wild. "Released gene diversity (GD) retained" is the amount of gene diversity retained relative to the released cohort of peregrines rather than just the ancestors of sighted or breeding birds. Inbreeding coefficients were calculated assuming unknown ancestors are unrelated founders and represents the minimum level of inbreeding.

| PARAMETER | Captive 1993 | Released 1982 to 1991 | Sighted | Bred | Bred 1992 | Bred |
|---|---|---|---|---|---|---|
| n | 128 | 544* | 102 | 74 | 39 | 54 |
| # of Founders | 59 - 128 | 59 - 128 | 41 - 74 | 38 - 67 | 38 - 67 | 38 – 67 |
| Mean Kinship | 0.022 | 0.035 | 0.025 - 0.050 | 0.026 - 0.053 | 0.032 - 0.062 | 0.026 - 0.052 |
| Gene Diversity Retained (GD) | 98% | 96% | 95-97% | 95-97% | 94-97% | 95-97% |
| Released GD Retained | | | 55 - 64% | 50-59% | 50-58% | 50-59% |
| Founder Genome Equivalents | 22.66 | 14.25 | 10.06-19.66 | 9.45-18.93 | 8.01-15.75 | 9.64-19.19 |
| Inbreeding Coefficient (with unknowns) | (0.014) | (0.022) | 0.009 | 0.014 | (0.015) | 0.008 |

* includes 13 Canadian released birds

## Analysis of success

### Success of founders

A founder's opportunity to contribute genetic material to the wild population is influenced by differential reproduction in captivity. When birds with unknown ancestry are removed from the analysis about 45% of the gene pool of the captive population is derived from ten founding birds (Table 2). Ten founding birds have contributed 50% of genes found in he released peregrines. Almost 59% of the gene pool of the falcons identified as

wild breeders can be attributed to ten founders. The most represented founders are not necessarily the same individuals in each case, however (Table 2).

Table 2. Percent contribution of true founders to the known genetic pool of captive, released, sighted, and breeding peregrines. Shaded values indicate the ten most represented founders in each subset.

| FOUNDER | CAPTIVE (n=128) | RELEASED (n=544) | SIGHTED (n=102) | BRED (n=74) | BRED 1992 (n=39) | BRED 1993 (n=54) |
|---|---|---|---|---|---|---|
| 257 | 7.74 | 10.02 | 9.05 | 9.28 | 8.15 | 9.59 |
| 256 | 7.74 | 9.86 | 9.05 | 9.28 | 8.15 | 9.59 |
| 215 | 1.72 | 6.41 | 6.90 | 6.99 | 7.30 | 6.31 |
| 238 | 4.84 | 3.39 | 6.03 | 6.43 | 6.74 | 5.10 |
| 239 | 4.84 | 3.39 | 6.03 | 6.43 | 6.74 | 5.10 |
| 203 | 2.26 | 3.82 | 4.68 | 4.41 | 5.06 | 4.61 |
| 202 | 3.98 | 3.96 | 4.43 | 4.04 | 4.49 | 4.13 |
| 222 | 3.98 | 3.96 | 4.43 | 4.04 | 4.49 | 4.13 |
| 264 | 1.94 | 2.34 | 4.19 | 4.41 | 3.93 | 3.40 |
| 294 | 1.51 | 2.34 | 4.19 | 4.41 | 3.93 | 3.40 |
| 205 | 2.42 | 2.40 | 3.08 | 3.31 | 3.65 | 3.76 |
| 206 | 2.42 | 2.40 | 3.08 | 3.31 | 3.65 | 3.76 |
| 259 | 3.01 | 2.55 | 2.89 | 2.85 | 2.81 | 3.03 |
| 260 | 2.37 | 2.51 | 2.89 | 2.85 | 2.81 | 3.03 |
| 200 | 0.86 | 1.89 | 2.71 | 2.21 | 2.55 | 1.94 |
| 201 | 0.43 | 1.73 | 2.71 | 2.21 | 2.25 | 1.94 |
| 258 | 1.29 | 2.63 | 2.46 | 2.21 | 2.25 | 1.94 |
| 210 | 1.29 | 2.55 | 2.46 | 2.94 | 2.81 | 2.91 |
| 262 | 0.43 | 2.47 | 2.46 | 2.21 | 2.25 | 1.94 |
| 211 | 0.43 | 2.22 | 2.46 | 2.94 | 2.81 | 2.91 |
| 22 | 0.00 | 0.99 | 2.46 | 2.21 | 3.37 | 2.91 |
| 261 | 0.43 | 1.73 | 1.97 | 1.47 | 2.25 | 1.94 |
| 220 | 1.08 | 1.93 | 1.48 | 0.74 | 1.12 | 0.97 |
| 61 | 0.00 | 1.97 | 0.99 | 1.47 | 2.25 | 1.94 |
| 208 | 3.55 | 3.02 | 0.86 | 0.92 | 0.56 | 1.21 |
| 270 | 2.69 | 0.72 | 0.25 | 0.37 | 0.56 | 0.49 |
| 236 | 2.80 | 1.44 | 0.00 | 0.00 | 0.00 | 0.00 |
| 255 | 2.69 | 0.25 | 0.00 | 0.00 | 0.00 | 0.00 |
| OTHERS | 31.26 (n=29) | 15.11 (n=32) | 5.81 (n=15) | 6.06 (n=12) | 3.07 (n=5) | 8.02 (n=12) |

Figure 2. Number of descendants identified in the wild versus number of descendants released from each true founder that had at least one descendant identified.

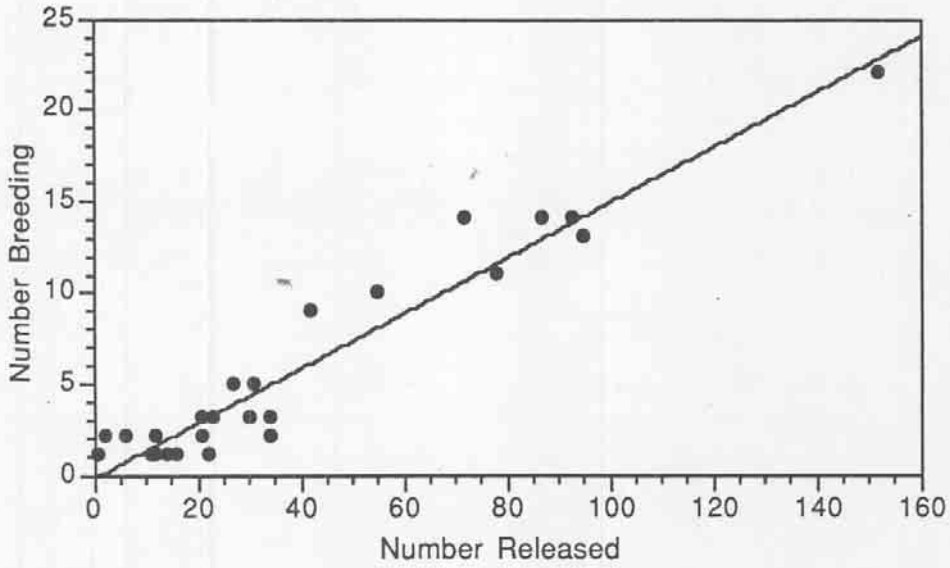
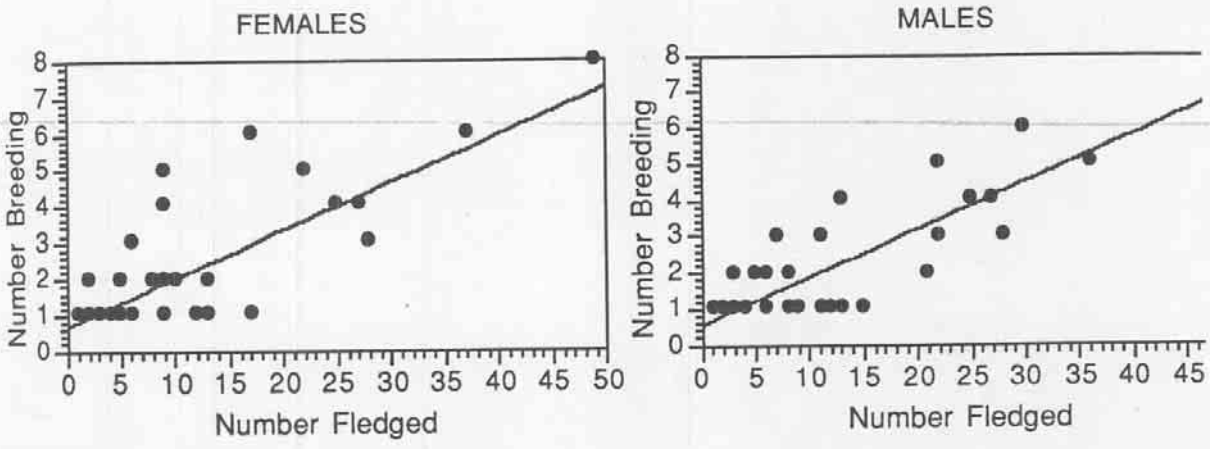



Figure 3. Number of offspring breeding in the wild versus number of offspring fledged by a particular bird that had at least one offspring breeding.



The fraction of genes contributed by true founders to the wild population is some indication of their suitability for producing descendants for the release project (Table 2) but this value does not reflect their performance relative to the number of descendants released. True founders appear to have descendants living in the wild in proportion to the number released (Fig. 2). However, founder success does not appear to be distributed evenly among progeny. In most cases, a true founder's success seems to be influenced by the success of particular offspring (Fig. 3).

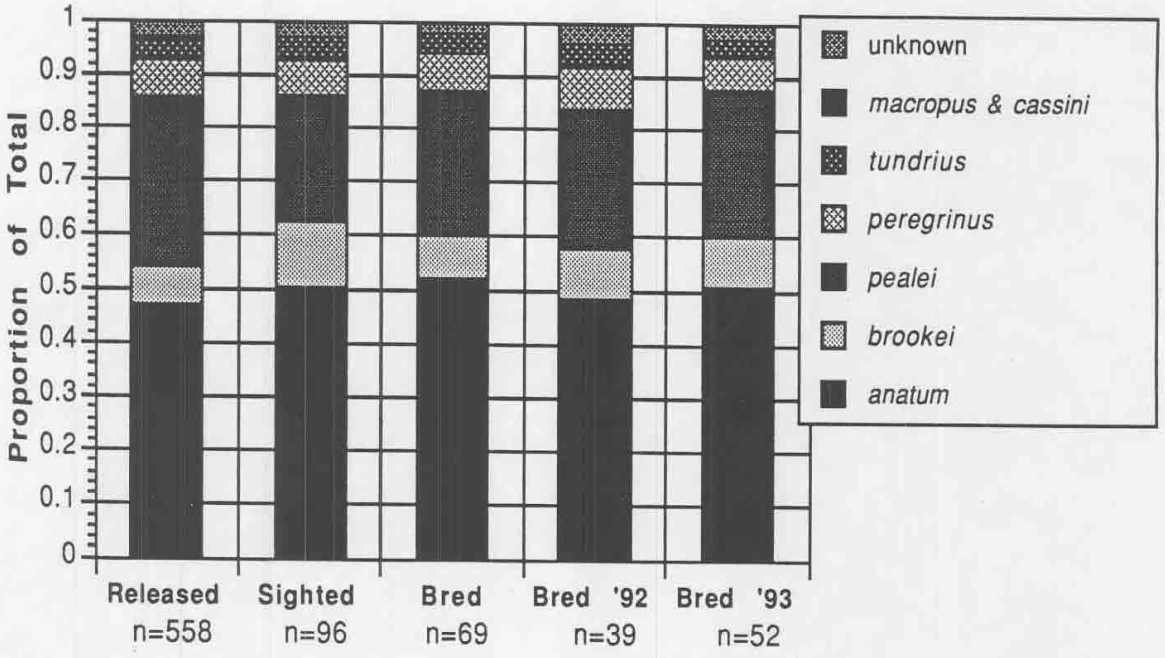
Subspecies status

As of 1993, the Peregrine Falcon population of the Upper Midwest has retained at least five out of the seven subspecies released. Approximately half of the genes released into the Upper Midwest through 1991 were *F. p. anatum* and about one third were *F. p. pealei ;* the remaining were *F. p. peregrinus, F. p. brookei, F. p. tundrius, F. p. cassini,* and *F. p. macropus* in order of decreasing magnitude (Fig. 4). Subspecies proportions in the breeding population are similar to those of the released birds (Fig. 4). However, the subspecific purity of founding birds has been diluted through hybrid coatings both in captivity and in the wild population.

Of 186 pure *F. p. anatum* birds released in the Upper Midwest through 1991, 11.8% were resighted after one year; 11.8% of 51 pure *F. p. pealei* birds have also been resighted. Discussions at the annual Midwest Peregrine Falcon Symposium in 1992 tentatively concluded that *F. p. pealei* falcons are not as well suited to life in the Upper Midwest as other subspecies since few were seen and none had bred after being released.

This conclusion is contestable now that four pure *F. p. pealei* falcons were identified while breeding in 1993.

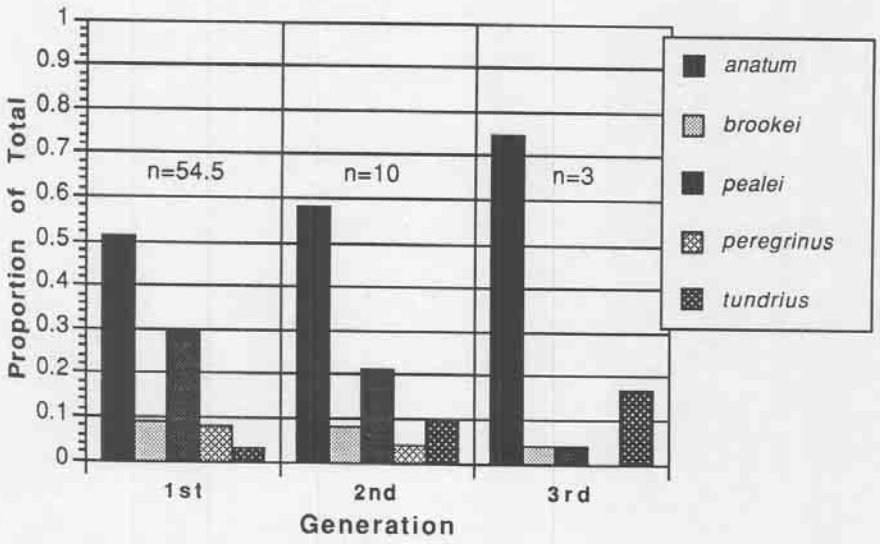
Figure 4. Representation of peregrine subspecies in the released, sighted, and breeding classes. Birds with fully unknown subspecies compositions are excluded from the analysis. The released birds were hacked or augmented to wild nests from 1982 through 1991. The sighted subset is made up of birds that were identified by band number one or more years after being released through 1993. The breeding subsets involve birds that were identified by band number breeding or attempting to breed in 1992 and 1993.




On the other hand, *F. p. pealei* genes seem to be disappearing rapidly from the second and third wild generations (Fig. 5). The breeding peregrines that were identified by band number through 1993 include three generations: 55 released birds, 11 offspring of released birds, and three offspring of wild-born birds. Although it is too early to detect true trends, the representation of *F. p. anatum* and *F. p. tundrius* appears to be rising with each

wild generation while the others are declining (Fig. 5). This apparent rend might reflect the differential success of particular birds more than particular subspecies, however.

Figure 5. Representation of subspecies in the breeding population by generation. The genetic composition of some birds was unknown and therefore removed form this analysis. Actual number of birds involved: 55 (first generation), 11 (second generation), and 3 (third generation). Sample sizes prevent the identification of an emerging trend. The differential success of particular birds greatly influences the representation of subspecies.



Influence of origin and rearing

The calculations in this section are based on falcons that were identified by band number. We assume that these falcons randomly represent the condition of the entire population. The number of birds resighted per attempt does not indicate survivorship since the birds that were sighted but not identified are not included in these calculations: For a discussion on survivorship, see Chapter 3.

The probability of resighting a wild fledged falcon (20 / 178 wild born and supplemented) was not significantly different from the probability of resighting a hacked bird (75/678) ($z=0.0658$, $df = 854$, $p < .90$). Of 68 hacking attempts (multiple uses of one hacking box in one year are lumped), the weighted mean number of birds resighted was $0.109 \pm 0.125$ birds per attempt . Wild adults fledged 67 broods. The weighted mean number of wild fledged peregrines resighted was $0.112 \pm 0.240$ birds per brood.

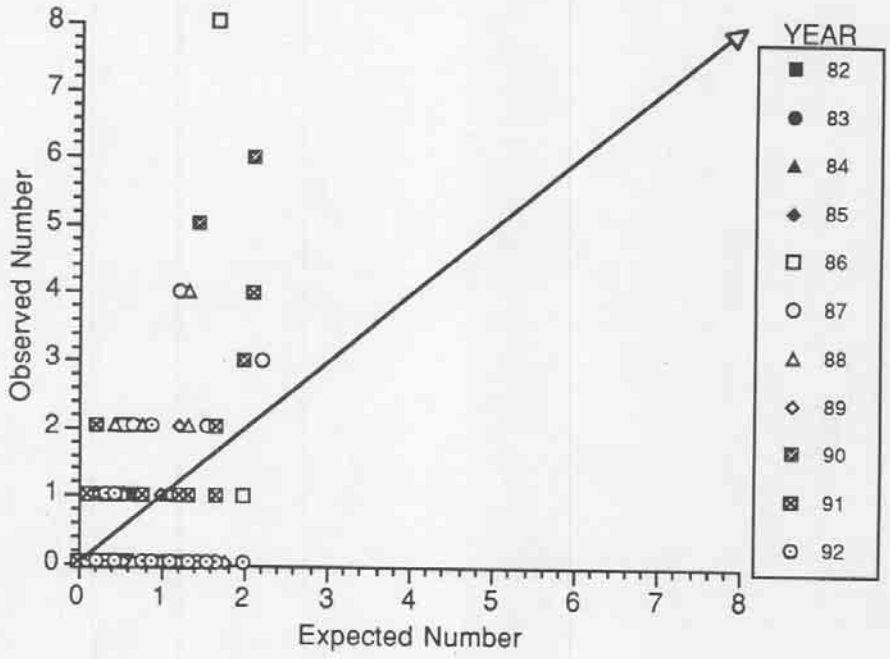
The probability of resighting released falcons (77 / 707 hacked and fostered young) was not significantly different from the probability of resighting wild produced young (18 / 149) ($z=0.4219$, $df = 854$, $p < .90$). Eighty-six release attempts were made between 1982 and 1992 (multiple uses of one hacking box in one year are lumped). The weighted mean of sightings was $0.109 \pm 0.166$ falcons per release attempt. Of 62 wild born broods with known outcomes, the weighted mean of birds sighted one or more years after fledging was $0.121 \pm 0.270$ birds per nest.

Survival of nest groups

The likelihood that a bird will be identified at least one year after fledging appears to be influenced by the sightings of nest mates (Fig 6, Appendix 2). Nests or

nest boxes from which at least one individual survived at least a year tended to produce more survivors than expected (Fig. 6). The number of resightings expected was calculated by multiplying the number of fledglings by the probability of an individual bird being resighted (94 / 856= 0.11). Between one and 20 birds fledged at a site from 1982 through 1992. The mean number of fledglings per site per year was 6.3 ± 4.8; the median was 4 fledglings.

Figure 6. Observed versus expected number of peregrines sighted at least one year after fledging per site per year. On average, sites where at least one bird survives tend to fare better than expected.



Lumping the 95 birds by site suggests that some sites, such as the Multifoods Tower in Minneapolis that had nine survivors compared to an expected 2.5, are highly successful (Fig. 7). This hides the fact, however, that eight of those nine, came from one year. Lumping survival by year indicates that the observed number of resightings per year is similar to what is expected, except for 1992 (Fig. 8). Given a mean breeding age of 2 years, we suspect that more birds from the 1992 cohort will be resighted as they establish breeding territories in 1994.

Figure 7. Observed versus expected number of falcons resighted after one year by site.

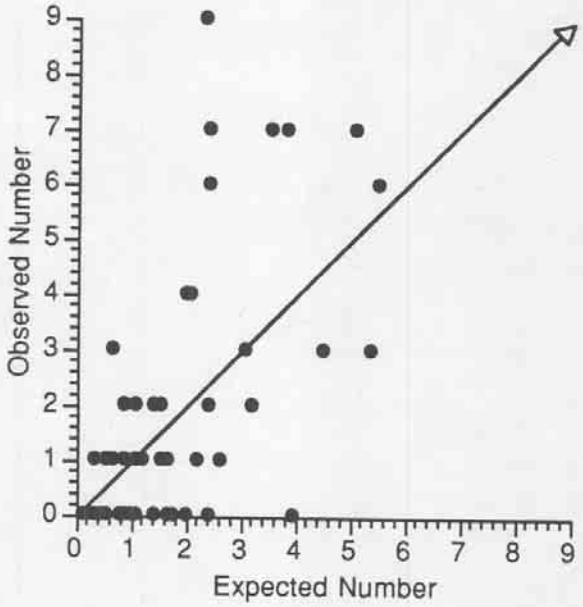
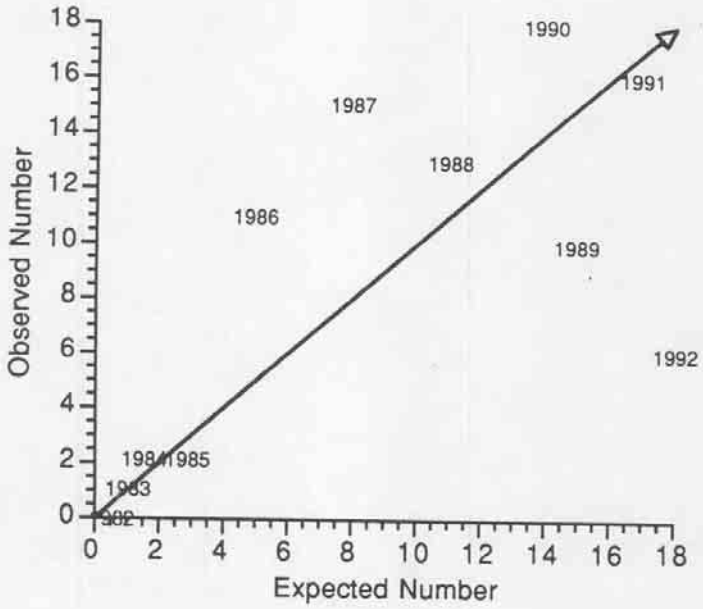


Figure 8. Observed versus expected number of peregrines resighted a year or more after fledging by year. 1992 does not accurately reflect the success of that cohort because of the relatively brief opportunity to resight surviving birds. Graph indicates that, barring 1992, annual site survival is close to expected values.




## DISCUSSION

### Genetic issues

The new peregrine population of the Upper Midwest shares a substantial proportion of its founding gene pool with the reestablished population on the East Coast. The East Coast project relied heavily on birds propagated by The Peregrine Fund, Inc. Although the Midwestern project relies on a number of private breeders throughout the U. S. and Canada, many of the peregrines breeding in captivity in the

United States have descended from The Peregrine Fund's original stock. The famous Heinz Meng's pair, siblings from British Columbia loaned to The Peregrine Fund, made up approximately 25% of the gene pool of birds that were established as breeders on the East Coast by 1985 (Temple & Cade, 1986). This same pair currently accounts for almost 20% of the known gene pool of birds that have or are breeding in the Midwest. The Midwestern population also shares founders with the peregrines released through Canadian restoration efforts. The majority of the pure *F. p. anatum* birds released into the Upper Midwest were supplied by The Canadian Wildlife Service facility at Wainwright through the Saskatchewan Cooperative Falcon Project.

The genetic relationships of the post-hatch-year peregrines identified in the Midwest during the summer of 1992 suggest the new population is engaged in a founding event. One falcon breeding in 1992 (MF-1) had three offspring and two grand-offspring represented in the 1992 identified breeding population. Of the 39 breeding individuals identified in 1992 for which both parents were known, 19 (48%) were full sibling to at least one other living bird in the wild.

Of the 28 unique breeding pairs for which both birds were identified and their parents known, one was a full sibling combination (U. S. Steel), one pair was half-siblings (NSP-Bayport) that became a mother-son combination in 1993. The frequency of close inbreeding (between full siblings and between parents and offspring) in natural populations of birds and mammals is generally below 6% (Ralls, Harvey, & Lyles 1986). The rate of close inbreeding in the Midwestern peregrine population (6.2%) is higher than reported for most studies of birds from which reliable rates can be calculated (Table 3).

Ten years after our release efforts began, the inbreeding coefficient of the 45 identified post- hatch-year birds in the Midwest ($F_{ib}$=0.012) was substantially lower than the inbreeding coefficient calculated for the 26 birds identified on the East Coast at a similar

phase of the release schedule ($F_{ib}$ = 0.09) (Temple & Cade, 1986). The potential for future inbreeding is high in the Midwestern population, however, because of its high kinship and small size. Ten years after the release efforts began on the East Coast, 73 nesting pairs were identified (Temple & Cade, 1986). Ten years after the Midwestern release program began for a second time, 33 nesting pairs were identified (Redig & Tordoff, 1992). A mean kinship between 2.6% and 6% is relatively high for a natural population. For reference, the kinship coefficient of siblings is 25%; first cousins have kinship coefficient 6.25%. Although no natural population has become extinct through inbreeding, research indicates that inbreeding depression is contributing to the demise, or impeding the recovery of several wild populations (Lacy 1993).

**Success**

Success does not seem to be influenced by whether the bird was hacked, fostered, or wild born. Subspecies does not appear to influence the success of a peregrine in the Midwest but this supposition warrants further investigation. The year in which a bird fledged does not appear to greatly impact its probability of surviving. The unusually low value for survivorship in 1992 (Fig. 7) probably reflects the length of time available to identify a survivor rather than relative survival.

Table 3*. Frequency of close inbreeding in natural populations of birds. The Mute swan value of 9.8% comes from a population founded by five escaped individuals. The unusually high value of 19.4% comes from a cooperatively breeding species in Western Australia. Sample sizes might reflect several breeding seasons. For example, the 74 pairs in this study are the sum of pairs where both birds were identified and parents known between 1987 and 1993 (1, 4, 7,9 , 12, 20, 21 respectively).

| SPECIES | PERCENT | SAMPLE SIZE | RESEARCHER |
|---|---|---|---|
| White-fronted bee eater | 0.0 | 81 | Emlen † |
| Pied flycatcher | 0.4 | 276 | Harvey & Campbell † |
| Florida scrub jay | 0.4 | 280 | Woolfenden & Fitzpatrick (1984) |
| Arabian babbler | 0.6 | 300 | Zahavi † |
| Yellow-eyed penguin | 0.6 | 490 | Richdale (1957) |
| Purple martin | 0.7 | 140 | Morton † |
| Great tit | 1.5 | 1000 | Greenwood, Harvey, & Perrins 1979 |
| Cliff swallow | 1.7 | 59 | Sikes & Arnold † |
| Acorn woodpecker | 3.2 | 218 | Koenig † |
| Mute swan | 9.8 | 184 | Reese † (1980) |
| Splendid wren | 19.4 | 211 | Rowley † |
| Peregrine falcon (Midwest USA) | 6.8 | 74 | this study through 1993 |

* Adapted from Ralls, Harvey, & Lyles (1986).
† Personal communication from investigators named to Ralls, Harvey, & Lyles (1986)

Despite the disqualified factors of rearing, subspecies, and year, peregrines in the Upper Midwest do not appear to survive by random chance. Although a larger sample size is needed to test this hypothesis, the data suggest that if one bird from a site survives a nest-mate is more likely to survive. The idea that nest-mates follow each other and thereby learn to move through the environment successfully might be worthy of further research. A similar argument was made for the success of the giant Canada Goose (*Branta canadensis maxima*) in the Midwest, which are also the result of release efforts (J. Cooper, pers. comm.). Sherrod (1983) found that peregrine families often pursued each other in mock combat and on feeding forays. He also speculated that peregrine families might migrate together from Greenland. Site success, however, does not account for the

unusually high number of resightings of released siblings (often from different release sites and sometimes out of different breeding facilities when captive pairs were traded). Olsen and Cockburn (1991) suggested the size and condition of the breeding female influences the sex of her offspring and thereby the probability that they will survive. Our data tentatively indicates that particular females and pair of birds are more successful that expected (Fig. 3). We conclude that the probability that a peregrine will survive in the wild is associated with both genetic and environmental conditions.

## RECOMMENDATIONS

Continued monitoring of the new peregrine population of the Upper Midwest is necessary for assessing how it emerges from its third founding event. The popularity of captive propagation-for-release programs makes information on successful efforts particularly valuable for both theoretical and practical conservation applications. Knowing the relationships of the new population is useful for decisions regarding releases and population management.

We suggest that any additional releases into the Upper Midwest continue to come from a captive population that is as genetically diverse as practical. If possible, the true founders that are currently underrepresented in the wild gene pool should dominate future releases. The Midwest peregrine recovery effort should continue to maintain accurate updates of the pedigree database. Effort should be made to gather information about the ancestry of the birds released through the Canadian Program since these birds mix with those in the United States and could be related to many of the birds released in the Midwest. There should be a comparative study between release projects to assess how closely the birds in the different programs are related and to evaluate the outcome of the

different release strategies. This information will be the baseline for future genetic research and studies concerning fragmentation of populations.

## ACKNOWLEDGMENTS

We are indebted to P. Redig for his leadership in restoring peregrines to the Midwest, for providing essential records, gathering information, and for his enthusiasm for this research. We are also grateful for the discussions and help provided by numerous peregrine breeders, especially R. Anderson, V. Hardaswick & D. Hunter of the South Dakota Raptor Trust, P. Harity of the Peregrine Fund, and L. Oliphant & P. Thompson of the Saskatchewan Cooperative Falcon Project. The assistance of R. Moen in data conversion, management, and manipulation is deeply appreciated as is the financial support of the U. S. Fish & Wildlife Service through M. Fuller and W. S. Seegar of the U. S. Army, The Minnesota Department of Natural Resources Non-game Wildlife Program, the Big Game Club Special Projects Foundation, the Graduate School of the University of Minnesota, the Dayton Natural History Fund and the Wilke Natural History Fund of the Bell Museum of Natural History, University of Minnesota. We also thank N. Flessness of ISIS for access to the beta-test version of SPARKS.

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# CHAPTER 2

# ANALYSIS OF DNA SIMILARITY

AND

# DNA FRAGMENT LOSS

IN THE

# PEREGRINE FALCONS BREEDING

IN THE

# UPPER MIDWEST

**ABSTRACT**

We used DNA fingerprinting and HRFLP analyses to quantify the genetic status of the re-established population of Peregrine Falcons in the Upper Midwest. The overall DNA similarity of the wild-breeding population as of 1992 was calculated as 36.42 $\pm$ 1.04(SD). Broken down by probe type, the DNA similarity was calculated as 36.21 $\pm$ 3.20(SD) for the DNA fingerprinting and 36.82 ± 2.94(SD) for the HRFLP analysis. The captive population, which gave rise to the wild one, had an overall DNA similarity of 32.99 $\pm$ 1.10(SD). Broken down by probe type, the DNA similarity for the captive population was calculated as 39.59 $\pm$ 1.22(SD) for the DNA fingerprinting and 21.86 $\pm$ 1.88(SD) for the HRFLP analysis. The DNA similarity index provides baseline data for future population assessment but does not adequately reflect current kinship levels as expected based on the result of research on other vertebrates. The unique combination of subspecies involved in the release project might account for the poor correlation between DNA similarity and mean kinship. Approximately 12% of the 63 fragments scored in and the two assumed to be in the captive population were missing from the group of falcons analyzed in the wild. Without intervention, the new population was theoretically expected to lose about 9% of the genetic diversity present in the released population. We recommend a DNA analysis of at least the five major subspecies involved in the release project to assess differences in the frequency of fragment occurrences. We also recommend continuation of DNA analyses of wildborn peregrines and their parents in the Upper Midwest to insure accurate pedigree records and enhance the baseline genetic information presented in this report.

## INTRODUCTION

DNA fingerprinting has been available as a technique for ecological research for less than a decade (Jefferys et al. 1985). Within this decade it has become a standard tool for exploring parent-offspring relationships of a variety of vertebrates. Less commonly and more recently, DNA fingerprinting has been used to assess genetic variability within and between populations (Lehman et al. 1992, Longmire et al. 1991, Gilbert et al. 1990, Kuhnlein et al. 1990, W. Shor pers. comm.). The desire to apply molecular techniques to species conservation has gained momentum. At the most recent Conservation Biology Meeting (Tempe, AZ June 9-12, 1993), about 22% of the presentations dealt primarily with genetic issues. Some statistical and technical limitations still plague DNA fingerprinting, however, and the implications of molecular results should be viewed with a clear understanding of the assumptions underpinning them (Table 4) (Lynch 1988, 1990).

Table 4. Limitations and assumptions underlying the results of DNA fingerprinting.

| |
|---|
| Statistical problems |
| 1) Generally unknown which fragments belong to which loci |
| 2) Generally unknown whether an individual is homozygous or heterozygous therefore the fraction of shared genes does not equal the fraction of shared bands, |
| Technical problems |
| 3) Comigration of unrelated fragments--inflates the variance of similarity |
| 4) Variation among used and non-used fragments may be different (Jeffreys et al. 1985), |
| 5) Some fragments may be linked and therefore not independent, |
| Assumptions |
| 6) Marker alleles are neutral and unlinked with selected loci and each other, |
| 7) Probability of mutation is negligible, |
| 8) Data is unambiguous; "This is not meant to trivialize the numerous aspects of gel running, reading, and interpretation which may sometimes rival the statistical problems (Lynch 1990 referencing Lander 1989)." |
| 9) Sample consists of random members of the population. |

Adapted from Lynch 1988, 1990

We used DNA fingerprinting and hypervariable restriction fragment length polymorphism (HRFLP) analysis to study the genetic diversity of the new population of Peregrine Falcons in the Upper Midwest. DNA fingerprinting detects polymorphisms in the variable number tandem repeat (VNTR) region of chromosomes, also known as minisatellite DNA (Fig. 9). VNTR's are repeating sequences of 15-30 base pairs. These regions serve as spacers (introns) that separate the areas of DNA that code for amino acids. The number of introns can be highly variable between individuals due to unequal crossing over during meiosis (Fig. 10A).

HRFLP's come from satellite DNA (Fig. 9). Satellite DNA is also referred to as heterochromatin, centromeric tandem repeats, or junk DNA. HRFLP's are repetitive sequences made of 150-200 base pairs and are thought to prevent the separation of chromatids until the outer arms of the chromosomes have duplicated. HRFLP's are more stable than VNTR's and polymorphisms are thought to be due to mutations at the restriction site rather than crossing-over events (Fig. 10B).

Figure 9. Representation of one of 25-26 homologous pairs of chromosomes found in Peregrine Falcons. The satellite region of approximately half of these pairs contains tandemly repeated HRFLP's that hybridize with the 175 base pair unit cloned from a Merlin. The VNTR regions found nearer the ends of the chromatids hybridize with cloned sequences from the Peregrine Falcon genome to create DNA fingerprint patterns.

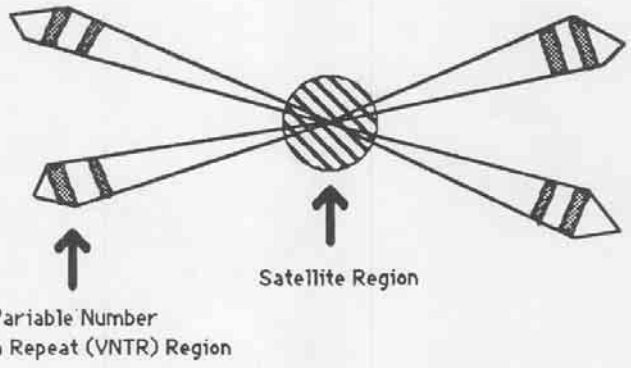
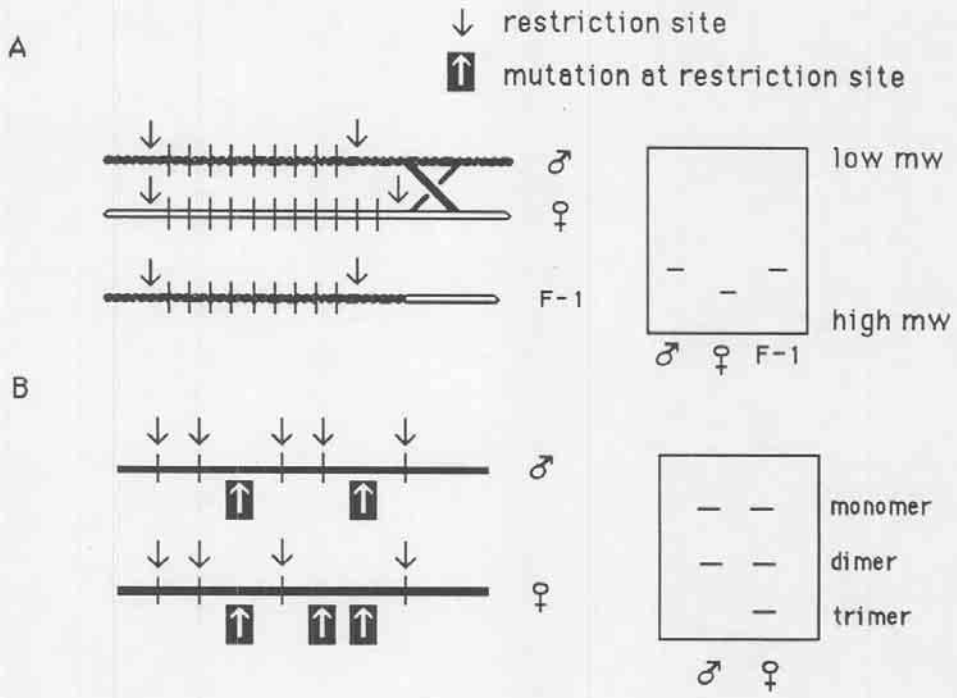


Figure 10. VNTR segment (A) and RFLP segment (B) of chromosome with corresponding autoradiograph patterns. VNTR segments are more likely to vary between family members due to unequal crossing over within repeats.




The Peregrine Falcons of the Upper Midwest are well suited for genetic study. The original population was extirpated in the middle of this century but restoration efforts beginning in 1982 have led to a small breeding population. Most of the identified breeders have reasonably complete pedigrees, many going back as far as the 1960's when their ancestors were brought into captivity for breeding. Additionally, breeding birds in the wild or their offspring were accessible for blood collection. We

also had access to DNA samples from many of the captive falcons used in the release project.

The intent of this research was to quantify the genetic variation in the new Peregrine population in the Upper Midwest as reflected by DNA similarity indexes based on DNA fingerprinting and HRFLP analysis. We also looked at differences in band frequency and band sharing between *Falco peregrinus anatum* and *F. p. pealei*, and between sexes. We compared band sharing data and band frequency information between captive birds and those that have bred in the wild of the Upper Midwest up to the end of 1992. As a side issue, we corrected or confirmed some of our suspicions about the paternity of some captive and wild birds using DNA fingerprinting and HRFLP analysis. We conclude this paper with a cautionary note and recommendations for monitoring the Peregrine Falcons in the Upper Midwest.

## METHODS

### Blood Collection and Purification

We collected and acquired blood samples from adult peregrines breeding in the wild, their offspring, and as many captive falcons related to the project as possible (Table 5). Since 1990, blood samples have been drawn from all peregrines released into the Midwest through The Raptor Center, University of Minnesota. See Appendix 3a for detailed' methods on blood collection procedures. Whole blood was stored in a lysis buffer (Appendix 3a) at room temperature for up to nine months.

Table 5. Types and numbers of blood samples from Peregrine Falcons. "COLLECTED " indicates the number of whole blood samples in our possession. Not all the samples collected from released birds and captive birds were used for DNA analysis; not all the samples used for DNA analysis produced usable results. Therefore, generally fewer DNA profiles were produced than the total number possible.

| TYPE OF SAMPLE | COLLECTED | USABLE FINGERPRINTS | USABLE HRFLPs |
|---|---|---|---|
| wild peregrines | 23 | 19 | 20 |
| wild eyases | 84 | 61 | 80 |
| 1990 releases | 83 | NA | NA |
| 1991 releases | 101 | NA | NA |
| 1992 releases | 106 | NA | NA |
| captive peregrines | 80 | 69 | 72 |

**DNA Fingerprints and HRFLP's**

DNA was purified out of the blood samples using an adaptation of the dialysis protocol described by Maniatis et al. (1982) (Appendix 3b). Aliquots of DNA were then cut with either Hae-III or Pvu-II, restriction enzymes found to produce variable banding patterns when used in combination with the appropriate probe (Appendix 3c). The DNA fragments produced by the restriction reaction were separated through an agarose gel and transferred to a nucleic acid binding membrane using the Southern blot technique (Southern 1975) (Appendix 3d). The membranes were probed with the appropriate probe made radioactive by nick-translation (Appendix 3e). After a 12-17 hour incubation time, the membranes were washed and exposed to x-ray film in a -600C freezer for three hours to several days, depending on the amount of DNA bound to the membrane. The x-ray films were developed and the resulting autoradiographs were stored for analysis (Appendix 3f).

We used the restriction enzyme Hae-III in combination with the peregrine probe pVPϕ1-3 developed by Jon Longmire at Los Alamos National Laboratory to isolate and detect the VNTR's (DNA fingerprints). The restriction enzyme Pvu-II was used in

conjunction with the Merlin probe PMR 1x4 (Longmire 1988). We also experimented with non-radioactive methods of detecting HRFLP's and VNTR's but were unable to detect peregrine DNA fragments using the Genius™ - Lumi-Phos™530 detection system from Boehringer Mannheim Corporation.

**Scoring Autoradiographs**

One-hundred-forty-nine usable DNA fingerprints and 172 usable HRFLP patterns on 36 unique autoradiographs resulted from the laboratory work (Table 5). We scanned autoradiograph patterns into computer images that were enhanced and trimmed in ADOBE PHOTOSHOP®. We then assigned a molecular weight to each band between 4000 and 51000 base pairs with the computer software NCSA GelReader® 1.0, from the National Center for Supercomputing Applications. NCSA GelReader assigned molecular weights to the bands based on standard lanes that were run two to four times on each gel. GelReader also assigned an intensity value to each band.

The computer-assigned weights had limitations both in accuracy and precision, especially between autoradiographs. However, the computer-assigned weights were useful references for assigning molecular weights to bands by hand. Molecular weights were manually assigned at least twice for each autoradiograph. Where discrepancies between the two hand-assigned weights existed, autoradiographs were rescored a third time. Intensity values were also reassigned by hand on a scale from 1 (faint) to 10 (darkest). The intensity values served as a criterion for including or omitting faint bands from the analyses.

After creating a pairwise DNA similarity index, we recompared falcons with a known kinship of 0.25 (full siblings or parent-offspring) and a DNA similarity of less than 20%. When necessary, adjustments were made to the assigned molecular weights.

**DNA Analysis**

The molecular weights and intensities assigned to DNA fragments were entered into a database along with basic falcon data (studbook number, sex, subspecies, parents, status, generation) . For the pVPφ1-3 probe, only bands given an intensity value of "3" or more were used in the analysis. For the PMR 1x4 probe, only bands given an intensity value of "4" or more were used in the analysis. Depending on the quality of the autoradiograph, bands with low intensities might not have been scored for all DNA samples. The frequency of occurrence for each molecular weight was calculated for three comparisons:

1) Male versus female,
2) *F. p*. anatum versus *F. p. pealei,*
3) Captive versus Wild-breeding populations.

Contingency table tests were performed on each set of comparisons to test for significant differences between the frequency of occurrence for each molecular weight.

For (both enzyme-probe combinations we calculated similarity with the equation:

$$S_{xy} = \frac{2n_{xy}}{(nx + ny)}$$

where "$n_{xy}$" is the number of bands shared by individuals "**x**" and "**y**". The number of I bands scored for an individual is represented by "**n**". Band-sharing data was analyzed with respect to known kinship to derive calibration curves for both probe-enzyme combinations. The apparent sex-linked fragments found in the pVPφ1-3 patterns prompted us to calibrate similarity curves by gender as well.

We compared the captive falcons and wild breeding falcons through mean similarity (S). Mean similarity is biased since it is composed of non-independent components. We calculated variance for S using a formula derived by Lynch (1990) that results in an unbiased estimate of variance in similarity:.

$$\mathbf{Var(S)} = \frac{N \quad \mathbf{Var(S_{xy})} + 2N' \ \mathbf{Cov(S_{xy},S_{xz})}}{N^2}$$

**N** is the total number of similarity measures used to estimate **S**. ***N'*** is the number of pairwise comparisons that share an individual. $\mathbf{Var(S_{xy})}$ was calculated with the formula:

$$\mathbf{Var(Sxy)} = \frac{2\bar{S}(1-\bar{S})(2-\bar{S})}{\tilde{n}(4-S)}$$

where **ñ** is the average number of bands exhibited by an individual. $\mathbf{Cov(S_{xy},S_{xz})}$ was calculated with the formula:

$$\mathbf{Cov(Sxy,Sxz)} = \frac{N' \ (\overline{S_{xy}S_{xz}} - \bar{S}^{2})}{N' - 1}$$

Comparisons between the captive and wild-breeding populations assume that the individuals sampled are representative of the entire population. The entire captive population consists of about 70 wild caught founders and approximately 210 of their descendants. Some of the captive birds died before blood samples were taken. Blood was not available from some living falcons, primarily because several private peregrine breeders were highly protective of

their breeding birds. We analyzed DNA samples from 80 out of an estimated 280 captive falcons.

In this paper, we define the wild-breeding populations as any peregrine that was known to lay or sire an egg that was laid in the wild. The entire wild-breeding population consists of approximately 104 birds of which 60 were identified before disappearing. We have analyzed blood samples from 23 wild-breeders. In ten instances, blood samples were not obtained from the breeding adult but blood samples from at least one offspring and one parent were available. The DNA patterns of three of these birds was inferred and used in the analyses based on the DNA patterns available from offspring, mates, and parents. Five falcons are represented only by the DNA of their offspring and are not included in the analyses discussed below.

## RESULTS

### Standardization of Gels

Standard fragments and one or more reference falcons were run on each gel making intra-autoradiograph comparisons possible. The same falcon was scored independently on two different gels for both probe-enzyme combinations. As expected, the band sharing index of the patterns resulting from the pVPφ1-3 probe was S = 1 (identical). The band sharing index of the patterns resulting from the PMR 1x4 probe was S = 0.75 (6 out of 8 bands were assigned identical molecular weights). The PMR 1x4 autoradiographs were recalibrated to correct the discrepancy.

**Fragment Inheritance**

For both probe-enzyme combinations, the DNA fragments used in the analyses appeared to be inherited in a Mendelian fashion. Out of over 20 family groups scored, all fragments could be attributed to either a bird's mother or father. For visual documentation of this assertion, see Appendix 4.

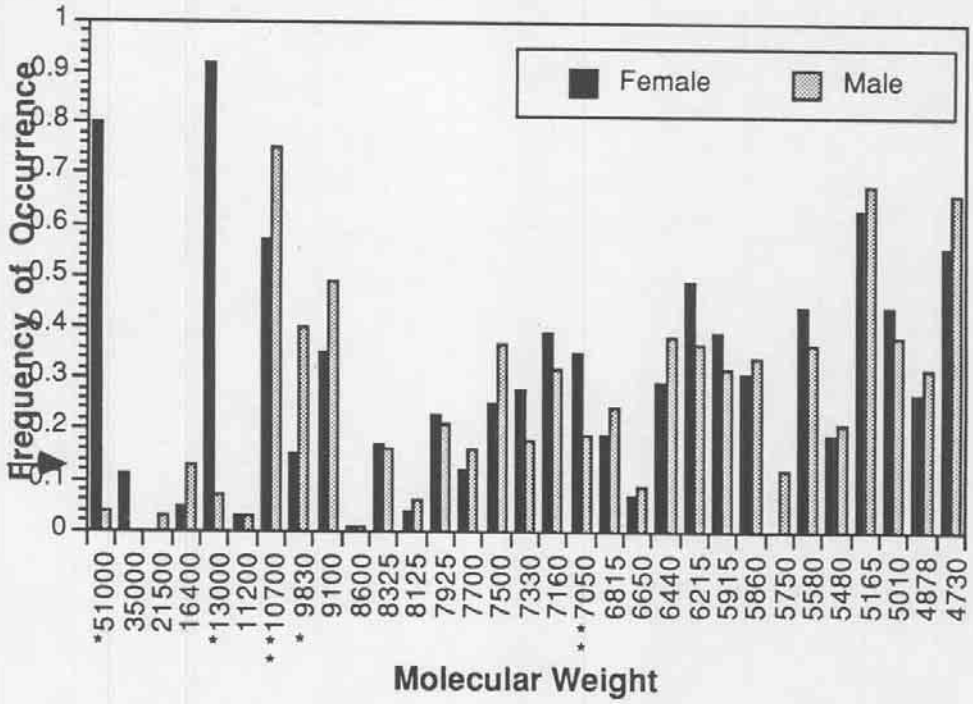
**pVPφ1-3 Results**

Frequency

From 152 autoradiograph patterns, 31 unique DNA fragments were scored between the molecular weights of 4700 and 51000. Between three and 13 fragments per bird were scored within this range of molecular weights. An average of 8.55 ± 2.03 bands were scored per individual.

When we grouped the data by gender, the average intensity of a particular fragment was similar between males and females but the frequency of band occurrence differed for some molecular weights. The high molecular weight fragments of 51000 and 13000 occurred almost exclusively in almost all female peregrines (Fig. 11). We suspect that the sex of the individuals recorded as males that have either of these fragments was misassigned at while attaching leg bands. Twenty two percent (5/23) of the statistically comparable frequencies of occurrences were significantly different with a confidence level of $\alpha = 0.01$ or more. Two rare fragments (21500 and 5750) were found only in males while one rare fragment (35000) occurred only in females.

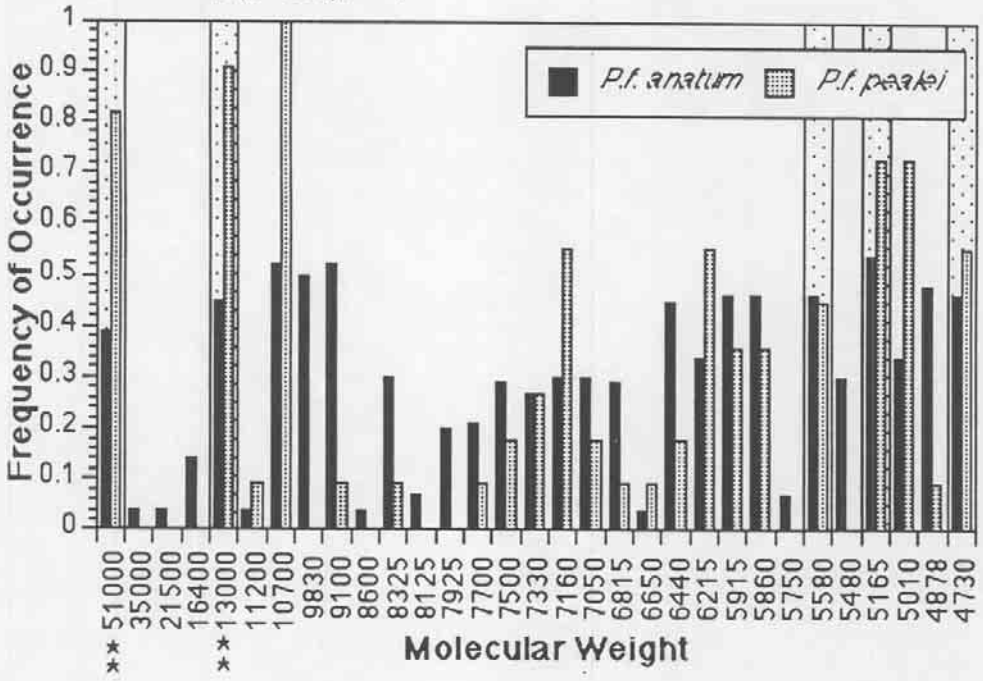
Figure 11. Frequency of fragment occurrence for the pVPϕ1-3 probe by gender. Sample sizes were n = 75 for females and n = 68 for males. * indicates a significant difference between genders for $\chi^2(\alpha = 0.05)(1\ d.f.)$. * * indicates a significant difference for $\chi^2(\alpha = 0.01)(1\ d.f.)$. Fragment comparisons below the arrow on the y-axis were too small to be tested statistically.




Sample sizes permitted only two out of the five pure subspecies for which we had at least one sample of DNA to be statistically compared. When pure *P. f. anatum* falcons (n = 56) were compared with pure *P. f. pealei* birds (n = 11), nine fragments occurred exclusively in *P. f. anatum* (Fig. 12). No fragments were exclusive to *P. f. pealei* but some fragment combinations might be indicative of the subspecies . Before drawing such conclusions, however, additional pure *P. f. pealei* DNA needs to be collected from wild birds and analyzed. Of the five molecular weights that could be

statistically compared, two (51000 and 13000) were significantly different at $\chi^2_{(\alpha = 0.01)(1\ d.f.)}$.

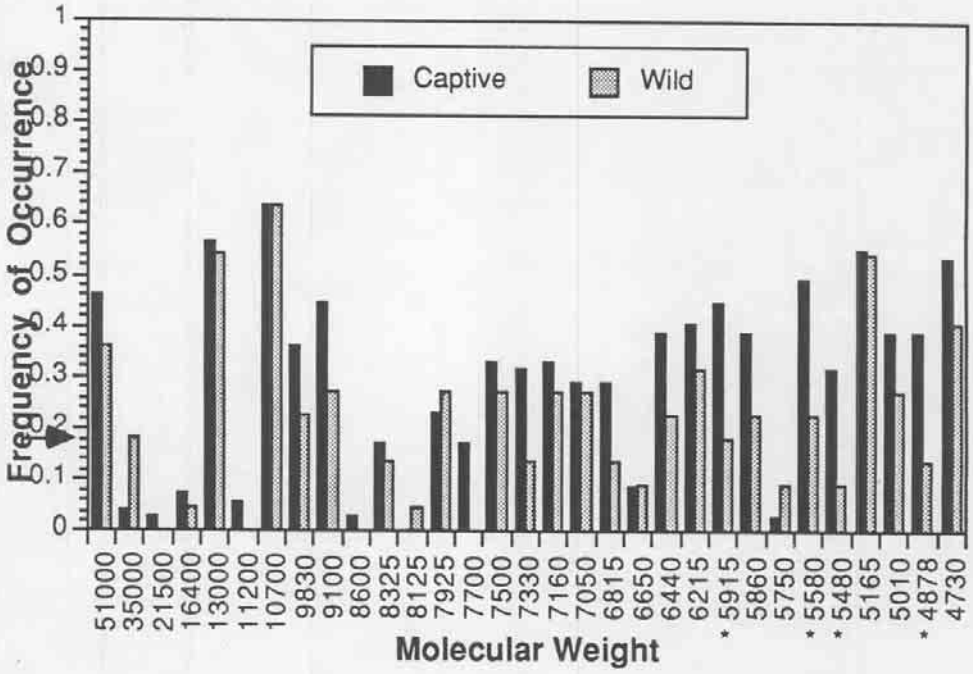
Figure 12. Frequency of fragment occurrence for the pVPϕ1-3 probe by subspecies. Sample sizes were n = 56 for *F.p. anatum* and n = 11 for *F.p.pealei* . The limited sample size for *F.p.pealei* permitted only the five shaded molecular weights to be statistically compared. ** indicates a significant difference between subspecies for $\chi^2_{(\alpha = 0.01)(1\ d.f.)}$.




The frequency of occurrence between the captive population (n=69) and those sampled from the wild-breeding population (n=22) differed significantly $\chi^2_{(\alpha = 0.05)(1\ d.f.)}$ for four out of the 21 fragments that were statistically comparable. Four rare fragments (21500, 11200, 8600,7700) were exclusive to the captive population while

one rare fragment (8125) was detected only in the wild breeding population (Figure 13).

Figure 13. Frequency of fragment occurrence for the pVPϕ1-3 probe compared between the captive and wild breeding population. Sample sizes were n = 69 for the captive population and n = 22 for the wild-breeding population. * indicates a significant difference between the populations for $\chi^2_{(\alpha = 0.05)(1}$ d.f.). Values below the arrow on the y-axis were too small to be tested statistically.

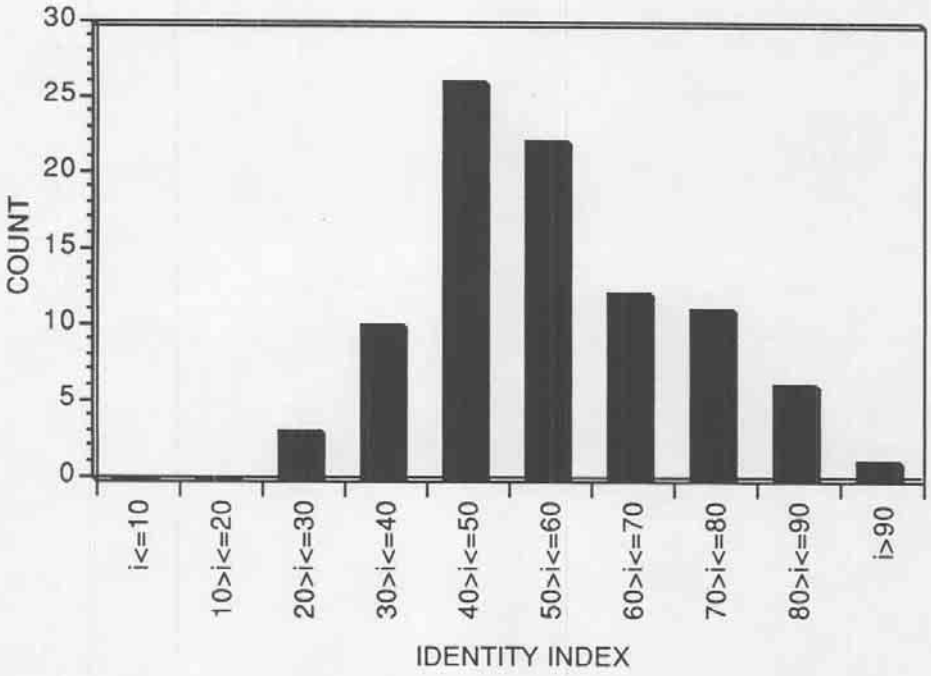



Kinship calibration and group similarity

The distribution of DNA similarity values approached normal for a particular level of kinship. For example, DNA similarity averaged 53.55 ± 3.25(SD) (n=91) for

pairs of birds with a kinship level equal to that of siblings or parent-offspring (Fig. 14). We created a calibration curve by plotting the average DNA similarity against known levels of kinship providing the number of comparisons at a particular level of kinship was greater than ten. The calibration curve was used to estimate the relatedness of the captive and wild groups of falcons (Fig. 15).

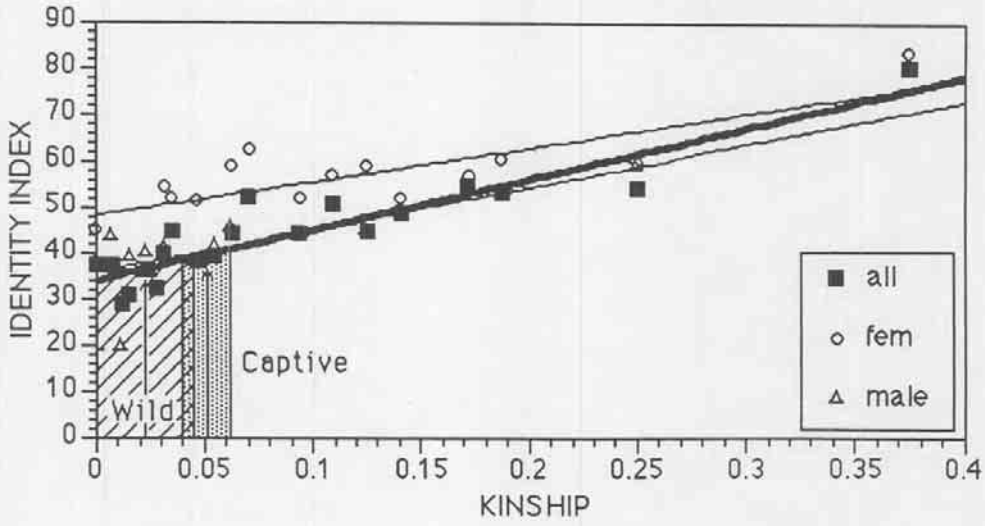
Figure 14. pVPϕ1-3 distribution of similarity values at kinship = 0.25.



The captive population of Peregrine Falcons had a similarity index of 39.59 ± 1.22(SD) (n=2346) using the pVPϕ1-3 probe. According to the calibration curve and disregarding gender, the captive population had an average kinship of about 0.051 (Fig. 15). When we used the standard deviation of the similarity index to approximate a range of probable kinships, kinship fell between 0.04 and 0.062.

The average DNA similarity index for the wild breeding population was 36.21 ± 3.20(SD) (n=231). The average DNA similarity corresponds with an average kinship of 0.022 on the calibration curve (Fig. 15). Kinships within one standard deviation of the calculated DNA similarity fell between 0.000 and 0.045. The DNA similarity indexes for captive and wild breeding populations were significantly different (t=32.48 (n=2577)).

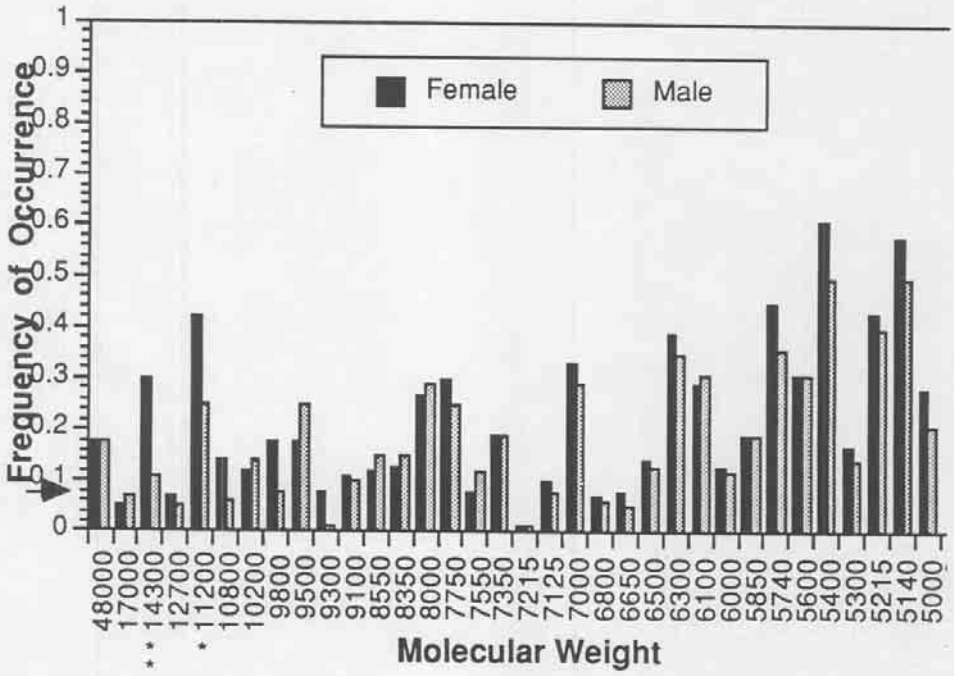
Figure 15. pVPϕ1-3 calibration curve and approximate position of the captive and wild breeding populations of Peregrine Falcons. Each point represents the average identity index for each level of kinship.



## PMR 1x4 Results

Frequency

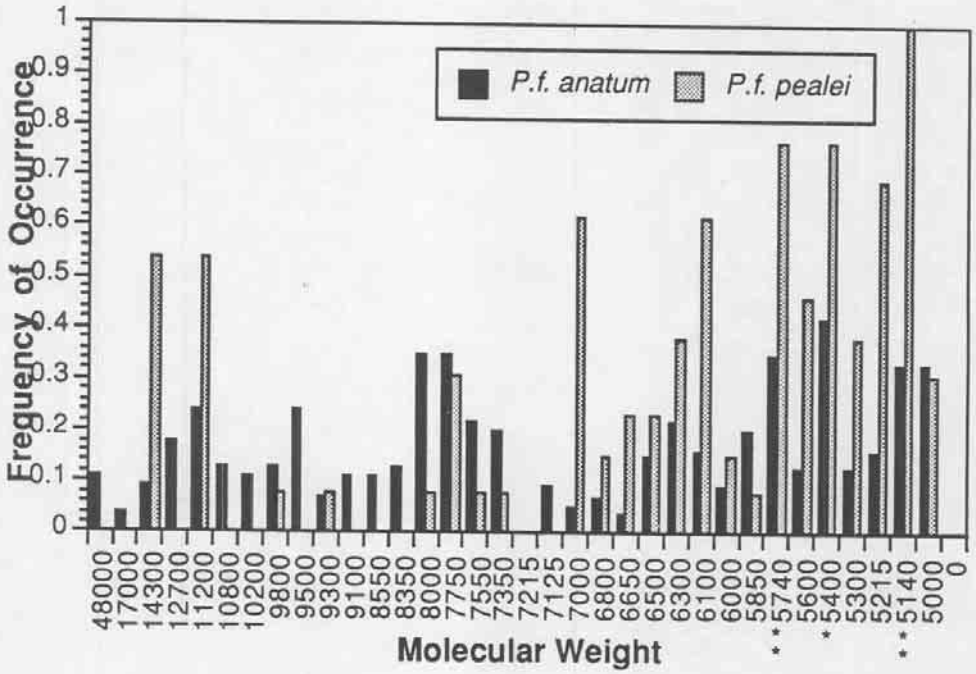
Figure 16. Frequency of fragment occurrence for the PMR 1x4 probe by gender. Sample sizes were n = 83 for females and n = 84 for males. * indicates a significant difference between genders for $\chi^2_{(\alpha = 0.05)(1\ d.f.)}$. * * indicates a significant difference for $\chi^2_{(\alpha = 0.01)(1\ d.f.)}$. When both frequencies are below the arrow on the y-axis the occurrence values were too small to be tested statistically.




Thirty-four DNA fragments were scored between the molecular weights of 5000 and 48000 on the autoradiographs made with the PMR 1x4 probe. Two individuals had no DNA fragments falling within the scored range. An average of 6.97 ± 2.54 bands were scored per individual. Excluding birds that had no fragments in the scored range, between 1 and 12 fragments were scored per peregrine. No DNA fragments were exclusive to a particular gender but two fragments (14300 and 11200) occurred

significantly more often ($\chi^2_{(\alpha = 0.01)(1\ d.f.)}$ and $\chi^2_{(\alpha = 0.05)(1\ d.f.)}$ ,respectively), in females (Fig. 16).

Figure 17. Frequency of fragment occurrence for the PMR 1x4 probe by subspecies. Sample sizes were n = 55 for *F.p.anatum* and n = 13 for *F.p.pealei*. * indicates a significant difference between subspecies for $\chi^2_{(\alpha = 0.05)(1\ d.f.)}$. * * indicates a significant difference for $\chi^2_{(\alpha = 0.01)(1\ d.f.)}$. Due to the limited sample size of *F.p.pealei* , only three molecular weights were statistically comparable; all three were significantly different.

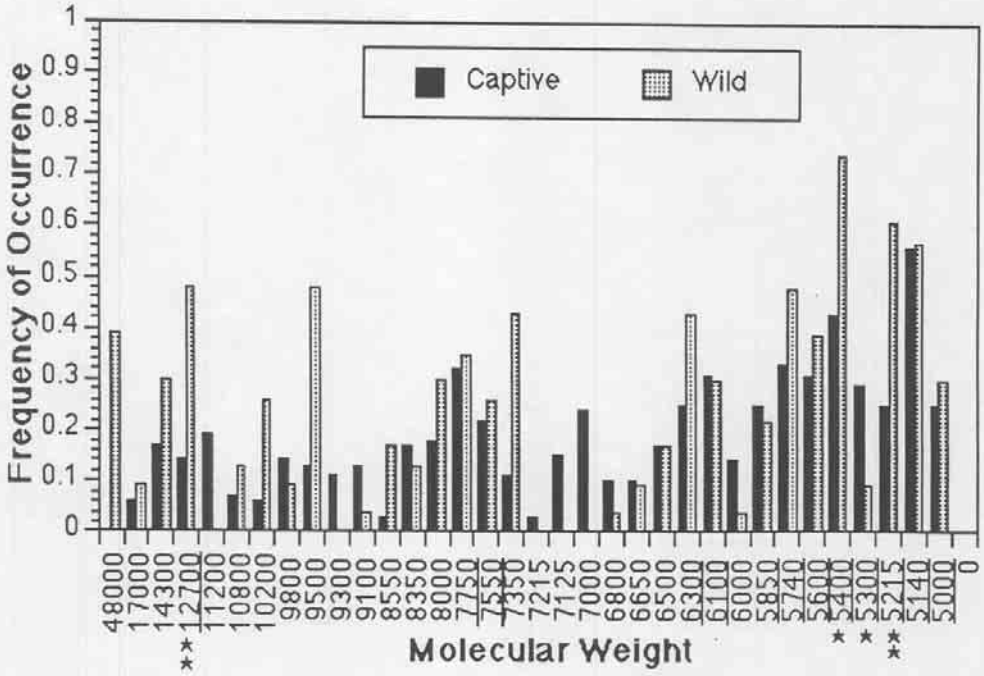



When the sampled peregrines were grouped by subspecies, differences in the frequency of fragment occurrence became apparent (Fig. 17). Only *F.p.anatum* (n=55) and *F.p.pealei* (n=13) subspecies could be statistically compared since the sample sizes of the three other pure subspecies for which we had DNA were too small. The frequency of occurrence for most molecular weights was too low for statistical analysis. However, the three molecular weights that could be statistically compared (5740,

5400, 5140) were significantly different (Fig. 17). Ten of the DNA fragments were found only in *F.p.anatum* birds. The two birds without fragments in the range we analyzed were also recorded as *F.p.anatum* .

When fragment occurrence was grouped by whether the birds were part of the captive or wild breeding population, four out of 13 statistically comparable molecular weights were significantly different for at least $\chi^2_{(\alpha = 0.05)(1\ d.f.)}$ (Fig. 18). Four fragments (9300, 7215, 7125, 7000) were exclusive to the captive population and one (48000) was detected only in the wild-breeding population.

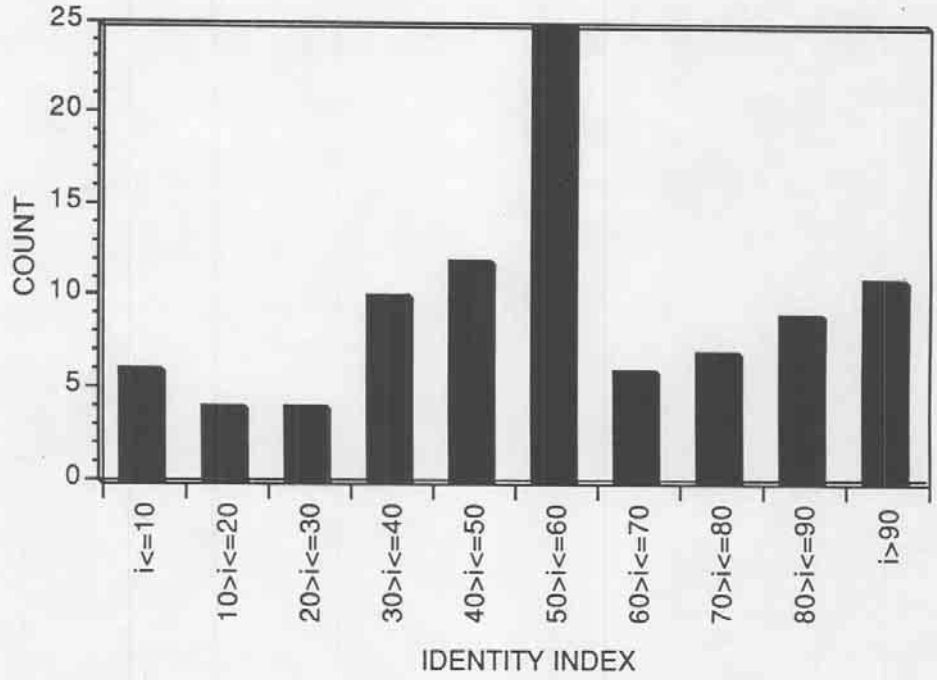
Figure 18. Frequency of fragment occurrence for the PMR 1x4 probe compared between the captive and wild population. Sample sizes were n = 72 for the captive population and n = 23 for the wild population. * indicates a significant difference between the groups for $\chi^2_{(\alpha = 0.05)(1\ d.f.)}$. * * indicates a significant difference for $\chi^2_{(\alpha = 0.01)(1\ d.f.)}$. The underlined values were the only molecular weights that could be statistically compared.



Kinship calibration and group similarity

DNA similarity values for the PMR 1x4 probe did not have a normal distribution for a particular level of kinship. The distribution of similarity at kinship = 0.25 is shown in Figure 19. At a kinship of 0.25 (siblings, for example), DNA similarity had an average value of 54.12 ± 3.65. The average similarity values for known levels of kinship were used to create a calibration curve for the PMR 1x4 probe (Fig. 20).

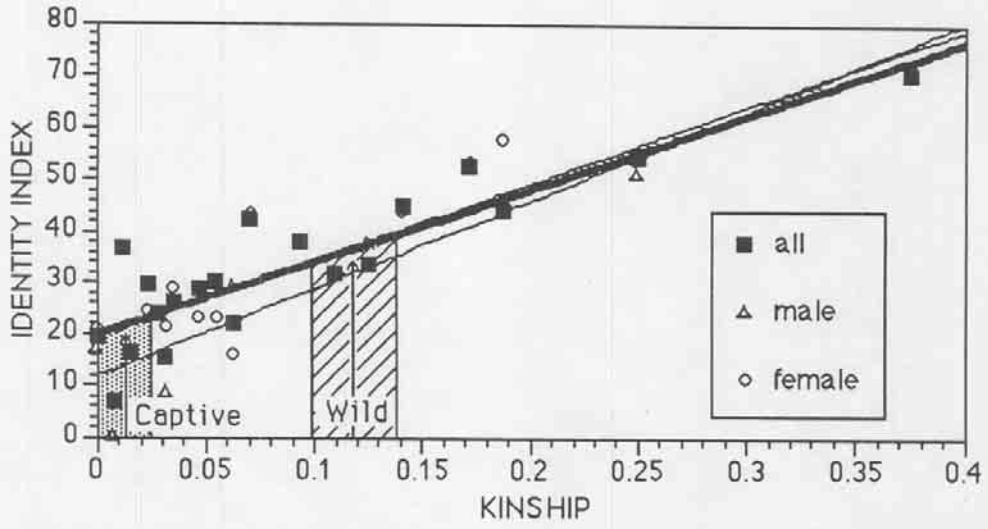
Figure 19. PMR 1x4 distribution of similarity values at kinship = 0.25.



The average DNA similarity for the captive population was calculated as 21.86 ± 1.88 (n=2556) using the PMR 1x4 probe. According to the calibration curve, a similarity value of 21.86 corresponds with a kinship level of 0.012. If the standard deviation associated with DNA similarity is used as an indicator of the range of kinship, kinship could fall anywhere between zero (unrelated) and 0.025.

The average DNA similarity for the wild population was 36.82 ± 2.94 (n=253). This DNA similarity yields a kinship estimate of 0.119. The range of kinship values included under the standard deviation of DNA similarity falls between 0.099 and 0.139 (Fig. 20). The DNA similarity of the captive and wild breeding populations were significantly different (t=5736 (n=2809)).

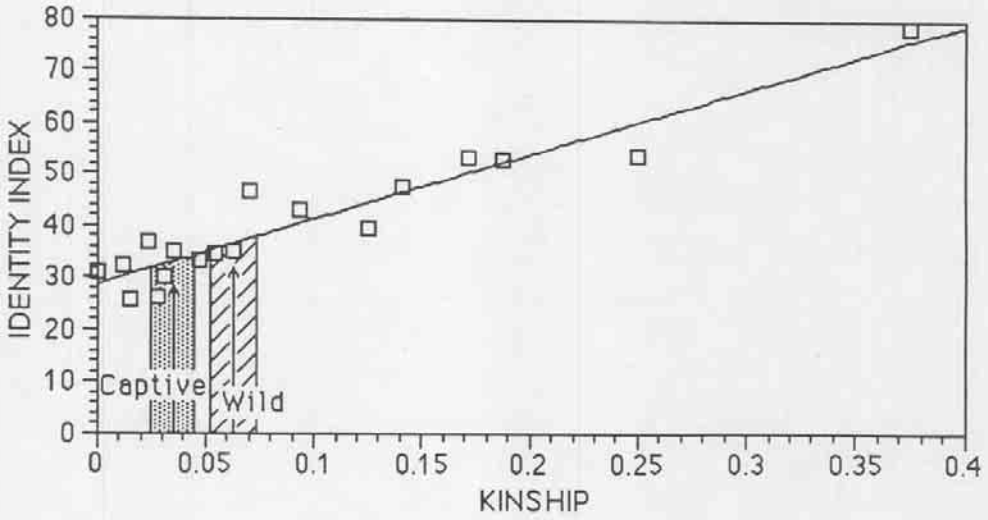
Figure 20. PMR 1x4 calibration curve with approximate positions of wild and captive populations superimposed.



## Combined Fragment Results

In an effort to increase the sample size of fragments used in the analysis, we combined the fragments produced by the two probe-enzyme combinations. When the data was combined, the average number of bands detected per bird was 15.60. We constructed a calibration curve in the same manner as the two discussed above except we did not separate males and females (Fig. 21). The combined DNA similarity for the captive population (n=1326) was 32.99 ± 1.10. The combined DNA similarity for the wild-breeding population (n=45) was 36.42 ± 1.04. When we used the combined calibration curve to estimate kinship, the captive population fell between a kinship level of 0.025 and 0.045. The mean kinship of the wild population was estimated to fall between 0.052 and 0.073 (Fig. 21).

Figure 21. Calibration curve and mean kinship estimates for the captive and wild breeding population based on the combined number of fragments and number of shared fragments for both probes.



## DISCUSSION

### Mean Kinship via DNA Similarity

The most surprising aspect of this study is the incongruity between the results of the mean kinship derived from each probe for the captive and wild-breeding populations. Theory suggests that the degree to which DNA similarity reflects kinship should be independent of the probe (Kuhnlein et al. 1990). Our results indicate, however, that the mean kinships estimated from the two types of genetic polymorphisms are not similar; nor do they approximate the results of the pedigree analysis.

A pedigree analysis which eliminated birds with unknown founders (Chapter 1), indicated the captive population of falcons have a mean kinship of 0.022. Calculations using the pVPφ1-3 probe overestimated the mean kinship of the captive population by assigning a range of kinships between 0.040 and 0.062. On the other hand, the results using the PMR 1x4 probe encompassed the mean kinship calculated by the pedigree analysis The PMR 1x4 probe had a mean kinship between 0.000 and 0.025.

Not surprisingly, the combined fragments produced an intermediate mean kinship ranging between 0.025 and 0.045.

Since fragments from the PMR 1x4 probe produced a mean kinship most similar to the one calculated from the pedigree information, one might assume it more accurately reflects mean kinship than do fragments from the pVPφ1-3 probe. However, the mean kinships calculated for the wild-breeding population suggest otherwise. From a pedigree analysis we found that the sector of the wild-breeding population for which we had DNA samples had a mean kinship of 0.05 (n=55) when birds with unknown ancestors were excluded from the calculations. If unknown ancestors are assumed to be founders, the mean

kinship of birds for which we have DNA samples could be as low as 0.025. The range of mean kinship derived with the pVPφ1-3 probe (0.000 to 0.045) ) encompassed the values calculated from the pedigree analysis. The range of man kinship derived with the PMR 1x4 probe (0.099 to 0.139) grossly exceeded other calculations. When the fragments scored for both probes were combined, the mean kinship estimated from the calibration curve (between 0.052 and 0.073) slightly exceeded expected values.

There dare several explanations for why the observed results differed from those that were expected. Violations of the assumptions 6 ,8 , and 9 listed in Table 4 probably caused some of the inconsistencies within the data.

Assumption 6--Fragments are neutral and unlinked with selected loci and each other: Although no effort was made to detect linked fragments outside of those associated with gender, it did appear as though the occurrence of several fragments was not independent. Linked fragments would inflate the DNA similarity indexes.

Assumption 8--Data is unambiguous:

After pain-taking and careful calibration and scoring of autoradiographs, rescoring, cross-comparisons, family comparisons, and rerunning entire gels and samples we cannot conclude that all our data is "unambiguous". Ambiguous data does not affect overall DNA similarity values as much as it could interfere with accurate calculations of kinship given the shallow slope of the calibration curves.

Assumption 9--Sample is random:

Our DNA samples from the captive population could be biased. Most of the birds used in the DNA analysis are from four breeding facilities which relied heavily on The Peregrine Fund, Inc. and the Canadian Wildlife Service at Wainwright for breeding sock. Two breeding facilities

in particular have supplied a number of birds directly or indirectly to the peregrine release project in the Upper Midwest but have not supplied us with DNA samples from their birds, to date. No effort was made to randomize our samples from the wild population, either. The small size of the population and the difficulty of catching breeding birds preclude efforts to adhere to rigorous statistical methods at present.

The peculiarities unique to the types of peregrines released into the Upper Midwest might also account for some of the incongruities in the DNA data. Although we were not Table to perform a thorough review of pure subspecies from the DNA samples we have, our analysis indicates it is clearly a mistake to assume there is no genetic difference between subspecies. Genes from at least seven different subspecies hove been released into the Upper Midwest. Genetic differences between subspecies for the fragments scored could lower the similarity index values making populations look more unrelated than they actually are if only one subspecies was involved. Furthermore, subspecies differences may make the calibration curves inaccurate depending on the representation of subspecies at each kinship level.

We have also assumed that the pedigree information made available to us is accurate. However, their is reason to speculate that not all of the information is accurate. In captivity, some females are artificially inseminated with sperm from several male. The paternity of their offspring is questionable unless DNA analyses are performed. Some breeding facilities assign a likely sire to a bird without proof of true paternity. In two instances, we have assigned paternity to peregrines with unknown fathers and in one instance disproved an assigned relationship. Analysis of wild birds has uncovered two cases of mistaken pedigrees in the three years we have been conducting DNA analyses. The most spectacular case is documented in Appendix 4. The second case occurred in

1991 at the East Chicago eyerie. The 1990 male was found dead under the eyerie in May of 1991 but was assumed to be the sire of the singly chick found in the nest that was tended by the female (see 1991 Annual Report for more details). Although we do not know who the true sire is, our DNA work indicated the 1990 male could not have been the chick's father.

**Fragment Occurrence**

If we (make the broad assumption that the birds we have sampled and fragments we have analyzed fairly represent genetic variability, a significant portion of variability has already been lost in the transition from captivity to wild-breeding. Approximately 12% (8 out of 65) of the scored fragments were absent in the peregrines representing the wild-breeding population. It is not surprising that most of these absent fragments occurred with a low frequency in the captive population. According to calculations based on pedigree information (see pedigree report), about 9% of the genetic diversity available in the captivity has been lost in the wild breeding population.

DNA fingerprinting and HRFLP analysis could be a useful way to monitor the loss of genetic information through the frequency of occurrence of fragments. This use of DNA fingerprinting, however, is subject to limitations. Fragments occurring at lower molecular weights than what we scored appeared to be less variable between individuals. By extending the range of molecular weights included in the analysis we probably would have reached the conclusion that a smaller percentage of fragments were lost in the wild-breeding population.

The two fragments that were observed only in the wild-breeding group reflect the biased nature of our sample of captive birds. We assume neither mutations nor crossing-over events created unique fragments in the regions of the genome that we examined.

## RECOMMENDATIONS

DNA fingerprinting and HRFLP analysis should not be used to estimate kinship in the peregrine population of the Upper Midwest. DNA fingerprinting and HRFLP analysis complement and strengthen the quality of pedigree information by ascertaining parentage. These molecular techniques could be used to supplement the pedigree analyses for the falcons of the Upper Midwest but not as a substitute a rigorous banding and monitoring program.

Although the subspecies composition of the Peregrine Falcon population of the Upper Midwest is unique compared to most reintroduction projects, we suggest caution when characterizing a small population solely on the basis of DNA fingerprinting or HRFLP information. To clarify if the combination of subspecies is truly affecting calculations of DNA similarity, further DNA comparisons should be done to on at least the *subspecies F.p. anatum, F.p. pealei, F.p. peregrinus, F.p. brookei, F.p. tundrius.*

**ACKNOWLEDGMENTS**

We are indebted to P. Redig for his leadership in restoring peregrines to the Midwest, for providing essential records, gathering information, and for his enthusiasm for this research. We thank J. Longmire of Los Alamos National Laboratory for teaching S. Moen the essential laboratory techniques and troubleshooting laboratory problems over the phone. We thank D. Foster and the late K. Guise for generously giving us access to their laboratories and equipment. We thank L. Foster, S. Tennyson and the graduate students and technicians in D. Fosters laboratory for assistance during the production of auto radiographs. S. Moen is particularly grateful to L. Foster for working with the radioactive probes while S. Moen was pregnant. We are also grateful for the blood samples, discussions, and help provided by numerous peregrine breeders, especially R. Anderson, V. Hardaswick & D. Hunter of the South Dakota Raptor Trust, P. Harity of the Peregrine Fund, and L. Oliphant & P. Thompson of the Saskatchewan Cooperative Falcon Project. Our thanks is also extended to R. Peifer of the General Biology Department who gave us access to the scanner and software necessary to convert autoradiographs into computer images. The assistance of R. Moen in data conversion, management, and manipulation is deeply appreciated as is the financial support of the U. S. Fish & Wildlife Service through M. Fuller and the U. S. Army through W. Seegar, The Minnesota Department of Natural Resources Nongame Wildlife Program, the Graduate School of the University of Minnesota, and the Dayton-Wilke Natural History Fund.

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# CHAPTER 3

## POPULATION VIABILITY ANALYSIS

## OF

## THE MIDWEST

## PEREGRINE FALCON POPULATION

**ABSTRACT**

The demographic parameters of the Midwest peregrine population are similar to those reported for other populations. Males and females first breed at an average age of 2.4 and 1.8, respectively. Roughly 1.78 young are produced per nesting attempt even though about 25% of nesting attempts fail: The annual adult mortality for females is 14%; for males it is 19%. We used the specific parameters calculated for the Midwest population as input data for VORTEX©, a model designed to simulate the dynamics of small populations. The results of the simulations reflect the high environmental variance associated with the demographic parameters precluding accurate predictions about population size. High environmental variance increases the likelihood of extinction. The simulations suggest that the continued success of the population is likely if all population parameters are accurate and static for the next 100 years. More information on juvenile survival would be instructive in fine tuning the model. Wit out management, the simulated populations had up to a 5.2% chance of becoming extinct within a century. Simulations of the data from the peregrine population in California confirm the modeled results of Wooton and Bell (1992). Additionally, we present extinction probabilities for the peregrine population in California.

## INTRODUCTION

Peregrine Falcons (*Falco peregrinus*) have been successfully released into the Upper Midwest through the Midwestern Peregrine .Falcon Restoration Project since 1982. The number of peregrines fledged into the wild per year ranges from five in 1982 to 186 in 1992 (Fig. 22). In all, approximately 882 falcons have fledged into the Upper Midwest. In 1986, the first recorded breeding attempt in the Upper Midwest occurred in more than 20 years in Alma, Wisconsin. Since then, a breeding population of peregrines has become established. A minimum of 41 pairs attempted to breed in the wild in 1993 (Redig & Tordoff 1993).

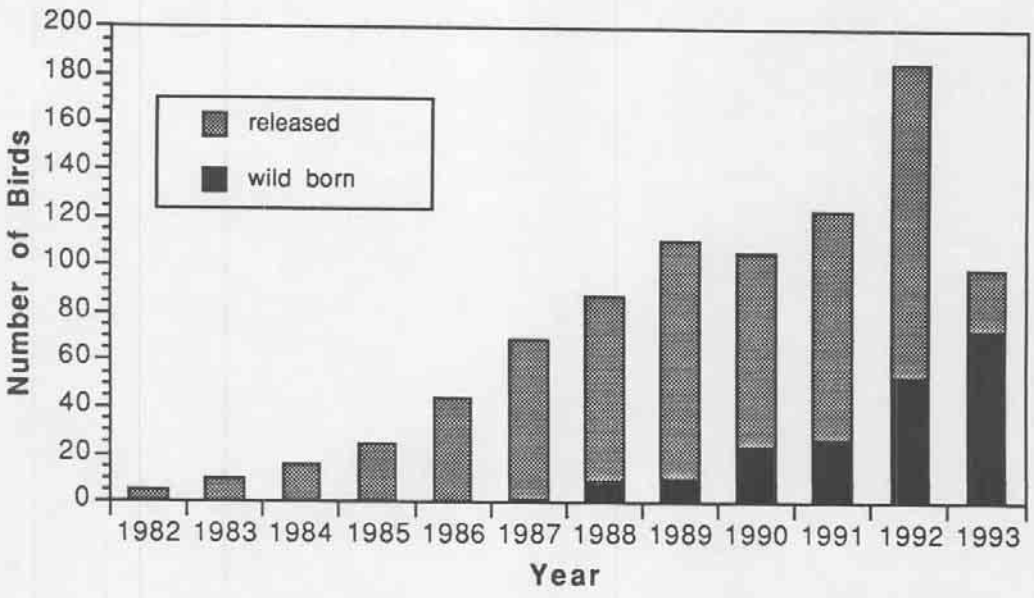
In this chapter we assess the probability that this new population will persist for at least one hundred years while retaining a reasonable amount of heterozygosity. To accomplish this task, we first calculate the population's demographic parameters. As a form of validation, we compare the demography of the Midwestern peregrines to values reported for other populations of Peregrine Falcons. The demographic parameters form the basic input for the stochastic population model, VORTEX© (Lacy 1992). We also analyze management strategies that might increase the probability that the new population will persist and thrive.

Unlike Wooton and Bell (1992), we suggest that it is more valuable to study the dynamics of small populations with a stochastic rather than a deterministic model. Stochastic models allow chance events (usually driven by a pseudo-random number generator acting on behalf of population parameters and environmental variance) to affect the population. Because chance plays an important role in stochastic models, no two outcomes are likely to be the same. A stochastic model should be run hundreds to thousands of times to derive accurate averages, standard deviations, and probabilities. Deterministic models project the most likely population trajectory by

using average demographic parameters but do not indicate the probability that such a scenario will occur. Deterministic models only need to be run once with a particular set of input since every outcome is the same.

For small populations environmental and demographic variability usually prevent "average" outcomes. Aside from senescence, virtually all events in the life an organism are stochastic (Lacy 1992). The fates of small populations are more often the result of chance events than mean birth or death rates and therefore show high variance around the mean. For the sake of comparison, we reanalyze the data in Wooton and Bell (1992) using a stochastic model.

Figure 22. Number of fledglings in the Midwest per year. 1992 includes 12 peregrines released in Nipigon, Ontario.



## DEMOGRAPHY

Figure 23. Map of Midwest population boundaries.


The Midwest peregrine population occupies a broad area from Kansas City, Missouri, to Winnipeg, Manitoba to as far east as Toronto, Ontario (Fig 23) . Juvenile dispersal is wide enough to suggest that birds have an opportunity to mix freely. However, about 40% of territorial birds identified between 1987 and 1992 defend areas on or within 25 miles of their natal grounds. The peregrines breeding in the wild

of the Upper Midwest share genes with neighboring populations because of the relatedness of release programs (see Chapter 1) and because of successful emigration arid immigration among populations. So far at least two peregrines have immigrated from eastern Canada, and one has emigrated to Saskatchewan. Although we have not analyzed their demographic status and ancestry in this report, the peregrines released in south-central Canada should be considered as part of the Midwestern population.

## Reproduction

### Age of first breeding

In this report, we define "breeding" as egg laying for a female and egg laying by a mate for a male. Of 882 young fledged into the wild over 11 years (Fig. 22), at least 101 have attempted to breed. This is a conservative estimate based on 82 identified and 19 unidentified birds. The mean age at first breeding for males is 2.4 ± 1.1 years (n=39, including two Canadian released birds). The mean age at first breeding for females is 1.8 ± 0.6 (n=37, including four Canadian released birds). These breeding ages are almost identical to those found in a peregrine population in Scotland that was expanding. In Scotland, males had an average first breeding age of 2.5 (n=6) and females had an average first breeding age of 1.9 (n=16) (Newton & Mearns 1988). In Alaska, where the population size is more stable, the mean first breeding ages were much higher; males bred at an average age of 2.9 (n=20) and females at 2.6 (n=5) (Ambrose and Riddle 1988). Estimates for the first breeding age in all reports, including this one, could be high since birds may have bred at other eyries prior to

identification. Strong breeding site fidelity in peregrines makes this an unlikely source of serious error, however.

In the Midwest, the median first breeding age is 2 years for both males and females. We found no indication that the mean first year of breeding is increasing in the Midwest. An increasing age of first breeding could indicate that the size of the population is stabilizing.

## Fecundity

Table 6. Number of wild-produced fledglings per year. Percentages and standard deviations (S.D.) were calculated from known outcomes from years 1989 to 1993.

| Number Fledged | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | Percent | S.D. |
|---|---|---|---|---|---|---|---|---|---|---|
| 0 | 1 | 3 | 4 | 3 | 3 | 6 | 10 | 7 | 24.95 | 6.92 |
| 1 | | 1 | | 4 | 4 | 5 | 4 | 7 | 22.78 | 7.44 |
| 2 | | | 5 | 1 | 4 | 4 | 1 | 10 | 16.29 | 9.99 |
| 3 | | | 1 | 2 | 2 | 5 | 8 | 11 | 21.75 | 6.92 |
| 4 | | | | 2 | 3 | 1 | 6 | 4 | 14.22 | 6.59 |
| unknown | | | | | | 1 | 5 | 2 | | |
| Total attempts | 1 | 4 | 10 | 12 | 16 | 22 | 34 | 41 | 140 | total |
| Total fledged | 0 | 1 | 13 | 20 | 30 | 32 | 54 | 78 | 228 | total |
| Fledglings per attempts when outcome known | 0 | 0.25 | 1.30 | 1.67 | 1.88 | 1.52 | 1.86 | 2.00 | 1.78 Average | 0.19 S.D. |

An average of 25% ± 7%(SD) of nesting attempts failed to produce fledglings in the Upper Midwest from 1989 through 1993 (Table 6). The success of nesting attempts in the Upper Midwest is similar to multi-year values found for peregrine populations in Arizona and The Northwest Territories and better than the average success of nests reported in other areas (Table 7). The variation in annual success is

lower than that calculated for other populations. Peregrine productivity in the Upper Midwest (1.78 ± 0.19(SD) fledglings per nesting attempt) is similar to other documented values (Table 7).

Table 7. Comparison of nesting success between Peregrine populations.

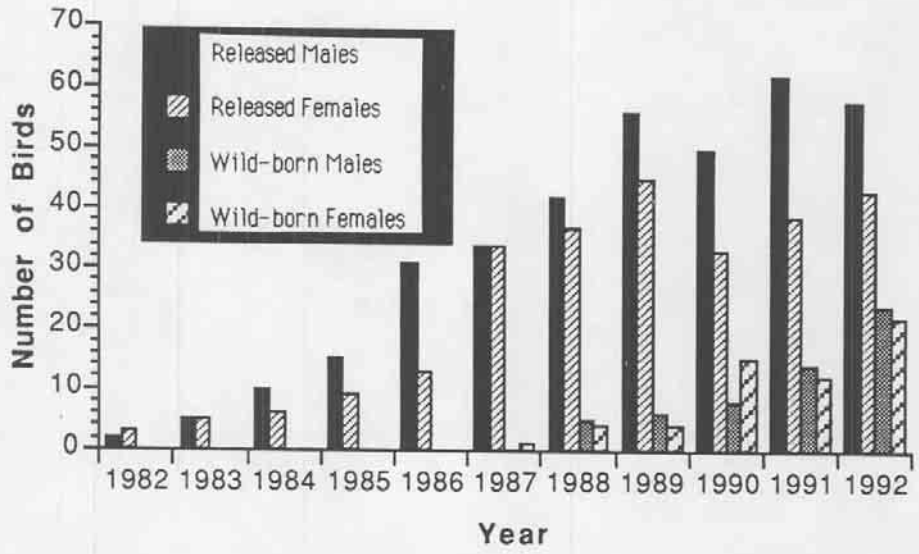
| % Successful Attempts | n | Young per Attempt | Year | Area | Source |
|---|---|---|---|---|---|
| 75.05 ± 6.92 | 117 | 1.78 ± 0.19 | 89-93 | Midwest, USA | This Study 1993 |
| 59.26 | 27 | | 1985 | Yukon | Mossop 1988 |
| 82.61 | 23 | 2.85 | 1985 | Ungava Bay, Quebec | Bird & Weaver 1988 |
| 58.88±14.26 | 222 | 1.20 ± 0.35 | 78-82 | Scotland | Newton & Mearns 1988 |
| 78.6 ± 22.91 | 73 | 1.86 ± 0.52 | 80-85 | MacKenzie River, NWT | Bromley & Matthews 1988 |
| 74.28±18.92 | 112 | 1.97 ± 0.67 | 81-86 | Rankin Inlet, NWT | Court et al 1988 |
| 73.00 | 126 | 1.70 | 76-85 | Arizona | Ellis 1988 |
| 52.00 | 25 | 1.20 | 1985 | Utah | Enderson et al 1988 |
| 55.63±13.64 | 58 | 1.49 ± 0.27 | 81-85 | Greenland | Falk & Moller 1988 |

Sex ratio

Half of the wild hatched young were identified as males (49.56%, n=115). On the other hand, males made up 55.66% (n=533) of all the released (hacked and fostered) young (Fig. 24). In 1986 significantly more males than expected were released ($\chi^2 = 3.68$, 1df). In other years, the sex ratio was skewed, but not significantly.

This deviation from the expected even sex ratio could be the result of several factors. Falconers are more likely to retain females for sport although none of the peregrine breeders supplying young for release in the Midwest claim to have done this. The gender of the eyases might be misassigned due to their young age at sexing; genetic evidence (Chapter 2) as well as field data (Redig & Tordoff pers. comm.) suggest that gender is not always assigned correctly. Olsen and Cockburn (1990) presented evidence that sex biases in peregrines living in Australia depended on the time which eggs were laid and weather. They conjectured that female size and condition in association with environmental factors influence the sex of their offspring.

Figure 24. Sex ratio of released and wild-hatched fledglings.



## Mortality

### First year

As calculated from band recoveries, the first year mortality of peregrines ranges between 55% Shor 1970) and 80% (Mebs 1960) (Table 8). An average of 66.7% first year mortality was assumed for the East Coast fledglings based on an observed pre--independence mortality of 26% coupled with an estimated 55% mortality from independence through the first year (Barclay & Cade 1983). Wooton and Bell (1992) chose a value of 64% $\pm$ 5% for the first-year mortality of the peregrine population in California. Newton and Mearns (1988) calculated a pre-breeding mortality of 56% for Peregrine Falcons in Scotland. They suggested if the population was stable rather than increasing and all other parameters remained the same, pre-breeder mortality would have to rise to 78%.

In the Midwest, first year mortality ranges between 57% and 67% assuming that observed adult mortality fairly represents true adult mortality. The high value (67%) is based on the assumption that all living birds older than two years of age (152 rounded to 160 to account for unknown but sighted birds) were sighted between 1984 and 1992. Since most birds are sighted during their second year, we inflated the actual number sighted by 17% (annual adult mortality) to compensate for pre-sighting losses. The low value (57%) additionally assumes that only 75% of the living adults have been sighted. This range of mortality is similar to that calculated by Newton and Mearns (1988).

The number of males and females resighted at least one year after fledging are in equal proportion to the ratio at which they fledged. Assuming that sighted

peregrines fairly represent the living cohort, we found no differential survival between sexes during their first year.

Table 8. Comparison of first year mortality between populations.

| MORTALITY | SUBSPECIES | SOURCE | METHOD |
|---|---|---|---|
| 57%-67% | n/a | this study | approximation from sightings |
| 55% | *F. p. macropus* (Australia) | Olsen & Olsen 1988 | band recovery |
| 56% | *F. p. peregrinus* (Germany) | Mebs 1971 | band recovery |
| 59% | *F. p. peregrinus* (Sweden) | Lindberg 1977 | band recovery |
| 71% | *F. p. peregrinus* (Finland) | Mebs 1971 | band recovery |
| 64% ± 5% | n/a | Wooton & Bell 1992 | estimate from other |
| 66.7% | n/a | Barclay & Cade 1983 | approximation from sightings |
| 70% | *F. p. anatum* (USA) | Enderson 1969 | band recovery |
| 80% | *F. p. peregrinus* (Germany) | Mebs 1960 | band recovery |

Adult

The overall annual mortality for peregrines in the Upper Midwest is 17% ± 7%. This is a weighted average based on resightings of 102 banded birds. We assumed that if a breeding bird did not return the following year, it was dead. Adult mortality is higher in the Midwest than in Australia and Scotland but lower than other rates reported for adult Peregrine Falcons (Table 9). In contrast with a population of

peregrines in France (Monneret 1988), the mortality rate for adult males is higher in the Midwest than it is for females (Table 9).

Like Newton & Mearns (1988), we found that adult mortality had high annual variance. Newton & Mearns (1988) suggest that their estimates of annual survival may have been atypically high because the population was increasing during the study. We suspect that survival will decline in the Midwest as the population stabilizes.

Table 9. Comparative annual mortality of adult peregrines.

| MORTALITY | SAMPLE | SUBSPECIES | SOURCE | METHOD |
|---|---|---|---|---|
| 17% ± 7% (all) | 102 | released | this study (87-92) | band identification |
| 14% ± 8% (female) | 49 | released | this study | band identification |
| 19% ± 9% (male) | 53 | released | this study | band identification |
| 5% | | *F. p. macropus* (Australia) | Olsen & Olsen 1988 | band recovery |
| 9% (females) | 75 | *F. p. peregrinus* (Scotland) | Newton & Mearns 1988 | capture-recapture |
| 11% (both sexes) | 83 | *F. p. peregrinus* (Scotland) | Newton & Mearns 1988 | capture-recapture |
| 19% | | *F. p. peregrinus* (Finland) | Mebs 1971 | band recovery |
| 23% ± 5% | | n/a | Wooton & Bell 1992 | estimate from other |
| 23% ± 15% (females) | 40 | *F. p. anatum* (Alaska) | Ambrose & Riddle 1988 | capture-recapture |
| 25% | | *F. p. anatum* (USA) | Enderson 1969 | band recovery |
| 28% | | *F. p. peregrinus* (Germany) | Mebs 1971 | band recovery |
| 32% | | *F. p. peregrinus* (Sweden) | Lindberg 1977 | band recovery |
| 43% | 104 | *F. p. pealei* (British Columbia) | Nelson 1988 | photo identification |

Longevity

The Midwest population has not been established long enough to set longevity records. So far two birds have lived at least eight years; both are females (one from Montreal 1984, the other from Multifoods 1985). Reports on longevity from other populations indicated that peregrines can survive more than a decade in the wild. The oldest male recorded in a wild population lived ten years and a female recaptured during migration to Greenland was at least twelve (Yates et al 1988). The oldest female recorded in the wild bred in Montreal for 12 consecutive years (1940-1952) making her at least 13 years old (Cade & Bird 1990).

## THE MODEL

To simulate the population dynamics of peregrines in the Midwest, we entered the demographic parameters into VORTEX, a computer simulation model developed in by R. C. Lacy of the Chicago Zoological Society. This model simulates the effects of deterministic forces in conjunction with demographic, environmental, and genetic stochasticity. VORTEX uses many of the same algorithms as the computer simulation program S GPC developed by J. Grier (Grier 1980, Grier & Barclay 1988) and a pseudo-random number generator based on the algorithm of Kirkpatrick and Stoll (1988). Vortex has been used extensively by the Species Survival Commission (SSC) of the International Union for the Conservation of Nature and Natural Resources (IUCN) to help guide the conservation and management of a variety of species ran in, from the Spotted Tree Frog (*Litoria spenceri)* to the Florida Panther *(Felis concolor coryi)* (Lacy 1992).

The standard deviations associated with the demographic parameters allow the results of each iteration to vary substantially. Validation runs of 50, 100, 200, 500, and 1000 iterations of the same input data indicate that 1000 iterations reduces the variation between runs to an acceptable level (percent extinction after 100 years--SD= 2%, intrinsic rate of increase [r]--SD=12%). Therefore, all scenarios discussed below were dun 1000 times.

**Standard Input**

The standard input file (Appendix 3) is based on the demographic information discussed above. We used two years as the mean age of first breeding and 12 years as the maximum breeding age. The initial population size (104) approximates the actual size and age distribution of the population in 1991. The carrying capacity of 250 individuals is based on the number of territorial birds believed to have occupied the Midwest before extirpation (50 pairs, Redig & Tordoff 1988) with allowances for non-breeder, and the availability of additional city nesting sites. We did not incorporate inbreeding depression or immigration into the model.

The most ambiguous demographic parameter, first year mortality, was assigned a five percent standard deviation and run at three levels: 57%, 62%, 67%. The value selected influences the outcome of the modeled population over the next 100 years (Fig. 25, Table 10). The simulations indicate that the growth rate of the population will stabilize after 10 years if juvenile mortality is low (57%). On the other hand, running the simulations with high first year mortality (67%) results in a probability of extinction of 5.2% and a final population size of 166 $\pm$ 70 (Fig. 25). The standard file produces a positive average rate of increase between r=0.013 $\pm$ 0.125 SD and r=0.073 ± 0.112 SD.

The probability of extinction is 5.2% or less in 100 years. The proportion of original heterozygosity left after a century is expected to fall between 0.87 ± 0.08 SD and 0.91 ± 0.02 SD).

Table 10. Results of 1000 iterations of modeled scenarios after 100 years. Supplementation was done by simulating the release of 64 chicks for 6 years.

| Scenario | r ± SD | Extinction Rate | N ± SD | $H_{exp}$ ± SD |
|---|---|---|---|---|
| Standard 57% | 0.073 ± 0.112 | 0.0% | 240 ± 20 | 0.91 ± 0.02 |
| Standard 62% | 0.045 ± 0.116 | 0.4% | 225 ± 34 | 0.91 ± 0.03 |
| Standard 67% | 0.013 ± 0.125 | 5.2% | 166 ± 70 | 0.87 ± 0.08 |
| No SD 57% | 0.079 ± 0.043 | 0.0% | 250 ± 4 | 0.92 ± 0.02 |
| No SD 62% | 0.052 ± 0.043 | 0.0% | 249 ± 5 | 0.93 ± 0.02 |
| No SD 67% | 0.022 ± 0.046 | 0.1% | 240 ± 22 | 0.91 ± 0.03 |
| Supplement 57% | 0.072 ± 0.111* | 0.0% | 239 ± 20 | 0.92 ± 0.02 |
| Supplement 62% | 0.046 ± 0.113* | 0.0% | 227 ± 33 | 0.92 ± 0.02 |
| Supplement 67% | 0.014 ± 0.120* | 1.8% | 173 ± 69 | 0.90 ± 0.05 |
| Fledglings =1.88 (62%) | 0.057 ± 0.115 | 0.0% | 233 ± 27 | 0.91 ± 0.02 |
| Fledglings =2.00 (62%) | 0.071 ± 0.114 | 0.0% | 239 ± 22 | 0.91 ± 0.02 |
| Fledglings =1.88 (67%) | 0.026 ± 0.121 | 2.5% | 202 ± 55 | 0.89 ± 0.06 |
| Fledglings =2.00 (67%) | 0.039 ± 0.112 | 0.3% | 218 ± 43 | 0.90 ± 0.04 |

* without supplementation

Removing the environmental variance (expressed as standard deviations around the demographic parameters) changes the behavior of the simulated populations (Fig. 26, Table 10). Without environmental variance, the probability of extinction becomes virtually zero despite different rates of juvenile mortality. The average intrinsic rate of increase becomes higher and more stable making nearly all populations reach carrying capacity by the 40th year. Removing environmental

variation improves the level of heterozygosity expected in the descendant population (Table 10).

Figure 25. Population growth over 100 years based on the standard input files.

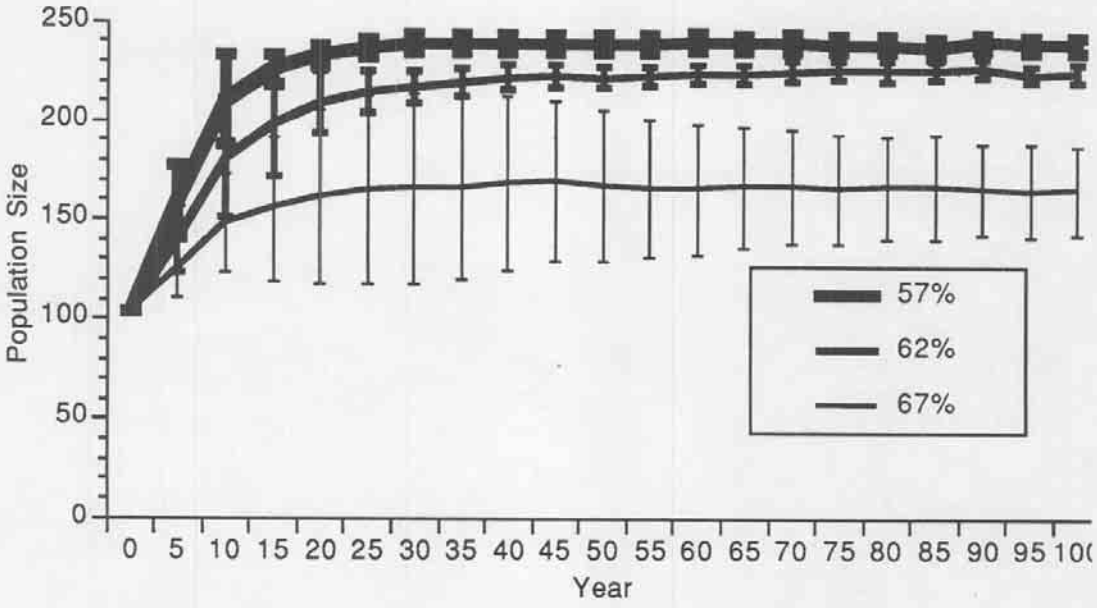
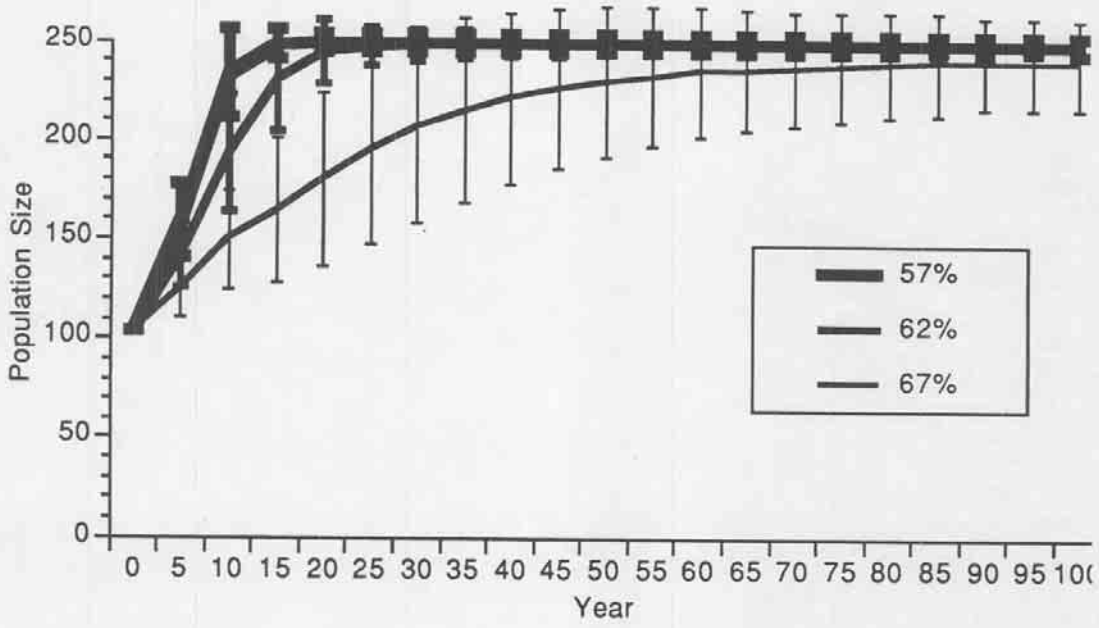


Figure 26. Standard files without environmental variation.




**Sensitivity analysis**

A sensitivity analysis investigates the influence particular parameters have on the population's behavior. Although sensitivity and elasticity are not necessarily rigorous mathematical terms, we define them here as they were in a study on the Californian peregrine population (Wooton & Bell 1992) for the sake of comparison. Sensitivity is the absolute change in growth rate per unit change of a demographic parameter ($\Delta\lambda / \Delta x$). Elasticity is the proportional change in growth rate to a proportional change in a demographic parameter ($x / \lambda)(\Delta\lambda / \Delta x$). We use "$\lambda$" (geometric rate of increase ) in place of Wooton & Bell's "R" (growth rate) so as not to confuse "R" with "$R_o$" (net reproductive rate per female), one of the output parameters

of VORTEX. The calculation for the deterministic λ is based on females only. Unlike the deterministic λ, the stochastic λ reflects the male portion of the population as well as environmental and demographic variation. These added variables can produce different values for λ (Table 11).

Sensitivity and elasticity indicate the relative importance of a change in an input value when all other values remain constant. The model is most sensitive to those parameters with the highest sensitivity and/or elasticity values. We note, however, that the assumption underlying this method of calculating sensitivity is inaccurate. The relationship between λ and changes in demographic parameters are not necessarily linear.

Table 11. Sensitivity of population growth rate (λ) to model parameters. Deterministic values are based on females only. The stochasitc values are based on the average of 1000 iterations. Variables are expressed in a way that is comparable to those discussed in an analysis of the Californian population (Wooton & Bell 1992). The value for fledglings is "the annual number of female fledglings per territorial female".

| VARIABLE | VALUE | | | λ | | SENSITIVITY | | ELASTICITY | |
|---|---|---|---|---|---|---|---|---|---|
| | Start | End | Change | Det | Stoch | Det | Stoch | Det | Stoch |
| Standard input-62% | | | | 1.106 | 1.077 | | | | |
| 1st year survival--female | 0.38 | 0.33 | 0.05 | 1.074 | 1.043 | 0.640 | 0.695 | 0.220 | 0.245 |
| 1st year survival --male | 0.38 | 0.33 | 0.05 | | 1.177 | | 2.001 | | 0.706 |
| Adult survival--female | 0.86 | 0.82 | 0.04 | 1.065 | 1.036 | 1.025 | 1.033 | 0.797 | 0.825 |
| Adult survival--male | 0.81 | 0.77 | 0.04 | | 1.003 | | 1.86 | | 1.398 |
| Fledglings | 0.89 | 0.94 | 0.05 | 1.120 | 1.059 | 0.280 | 0.359 | 0.225 | 0.297 |

Calculations using the deterministic growth rate indicate the modeled population responds most pronouncedly to changes in adult female survival. The survival of first year females appears to be more important than the annual number of

female fledglings per territorial female in dictating a deterministic population trajectory. On the other hand, the nature of the stochastic growth rate is more dependent on male survival (Table 11). Since adult male survivorship is lower than that of females, the suggestion that the population trajectory is most sensitive to changes in male survivorship is logical.

**Management**

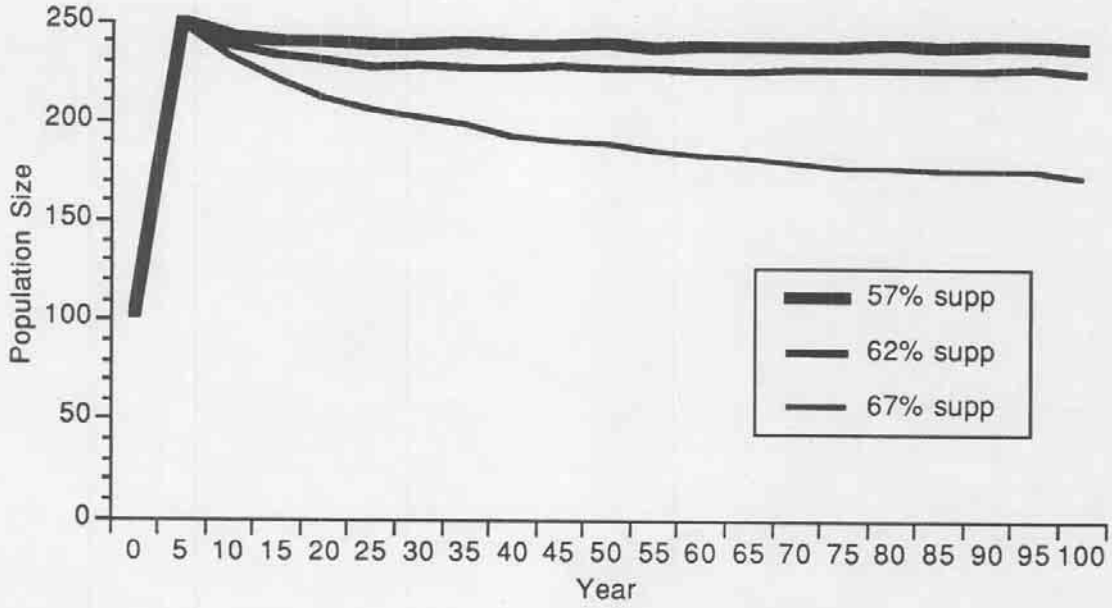
Even though the population is most sensitive to changes in adult mortality rates, it is most feasible to focus on management efforts on the number of young. Adult survival would be difficult, if not impossible, to increase. Juvenile mortality might be decreased by bringing fledglings into captivity for their first year and releasing them the following spring. However, this would be both a costly and risky strategy. Not only would the stress of capture and confinement be a potential source of mortality but the risk of disease, the impact of catastrophic events, and the potential decline in survival skills would increase. We modeled what we suggest are the most practical methods for assuring the population's continued success:

1) Hack additional birds into the wild or,
2) Supplement broods that have less than four chicks.

Nearly 100 peregrines have been hacked into the wild each year for the last several years. Continued hacking of about 32 females and 32 males every year for the next six years does not increase the size of the population or the chance that the population will persist (Fig. 27, Table 10). At higher rates of first year mortality, the

benefit of continued hacking is greater. However, the overall trend is similar to that shown in simulations that do not incorporate additional hacking.

Figure 27. Population trajectories for three levels of juvenile mortality with 64 birds released annually for six more years.



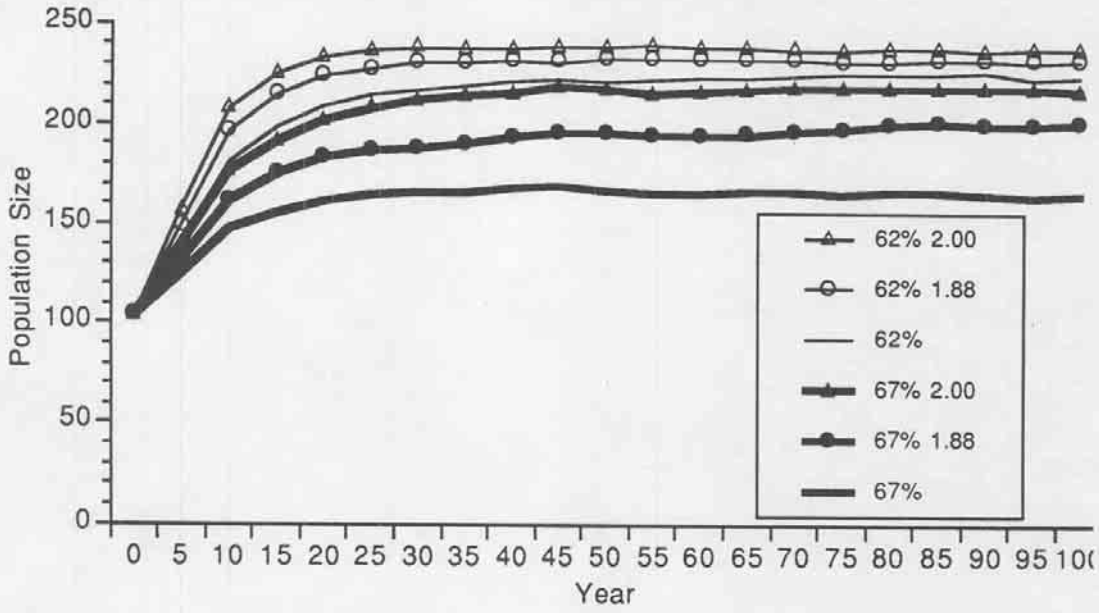

## Supplementation

A second way to manage the population is by augmenting young to nests with less than four young. Young for augmenting could be obtained by purchasing chicks from peregrine breeders or by inducing some wild pairs to lay a second clutch each year. Four young could probably be successfully raised to independence in most

nests. However, research suggests raising more than two chicks increases adult mortality (Nelson 1988).

We explored two levels of supplementation by raising the number of fledglings per nest from 1.78 to 1.88 and to 2.00. The effect of increased nest success has an impact on the size of the population as well as on the population extinction rate. The outcome of fledging an average of two young per nest impacts a population with a high juvenile mortality more than a population with a moderate juvenile mortality (Fig. 28).

Figure 28. Population trajectories with elevated number of fledglings. a=standard input (1.78 fledglings per nesting pair), b=(1.88 fledglings per nesting pair), c=(2.00 fledglings per nesting pair).



**California Population**

Wooton and Bell (1992) developed a model to simulate the population growth of the peregrine population in California. Their deterministic model did not allow them to explore the probability that the population would persist. Given the almost certain demise of the population without continued release efforts (based on their demographic assessment) made such an analysis redundant. Never-the-less, we have reanalyzed their data within the confines of VORTEX (Appendix 6).

VORTEX appears to be more sensitive to changes in demographic parameters than Wooton and Bell's model. Adding stochasticity dramatically decreases the model's sensitivity (Table 12) to mortality and fecundity rates, suggesting that variance buffers the impacts of changes in demography. Our sensitivity analyses supports results of Wooton and Bell indicating that the Californian population would be most sensitive to changes in adult mortality.

Our mean results are similar to their unstructured and spatially structured models (Fig. 29). The small differences between our population trajectories and the ones they document could be attributed to peculiarities between the input values needed by two programs. The standard error in the size of the extant population in our analysis suggests that the Californian population's fate is more predictable than the fate of the Midwestern population if no management activities are employed. All iterations of the Californian population were extinct within a century (Fig. 29, Fig. 30).

Table 12. Sensitivity of Californian population growth rate (λ) to model parameters. Deterministic values are based on females only; the values in parentheses are taken directly from Wooton & Bell 1992. The stochasitc values are based on the average of 1000 iterations. The value for fledglings is "the annual number of female fledglings per territorial female".

| VARIABLE | λ | | SENSITIVITY | | ELASTICITY | |
|---|---|---|---|---|---|---|
| | Det | Stoch | Det | Stoch | Det | Stoch |
| BASIC | 0.951 (.957) | 0.907 | | | | |
| 1st year mortality--female | 0.972 | 0.916 | 0.52 (0.42) | 0.23 | 0.20 (0.16) | 0.09 |
| 1st year mortality--male | | 0.918 | | 0.27 | | 0.11 |
| adult mortality--female | 0.981 | 0.919 | 1.00 (0.84) | 0.40 | 0.81 (0.68) | 0.34 |
| adult mortality--male | | 0.920 | | 0.43 | | 0.36 |
| fledglings | 1.000 | 0.968 | 0.24 (0.22) | 0.30 | 0.18 (0.16) | 0.23 |

Figure 29. Reanalysis of the 100 year trajectory of the Californian population of Peregrine Falcons.

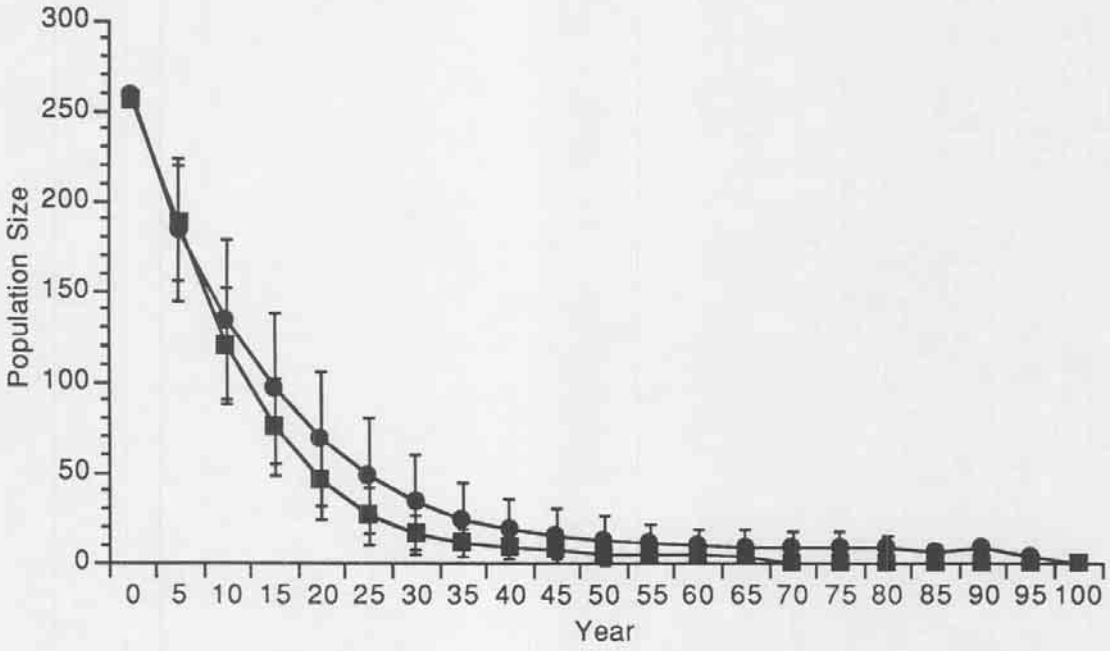
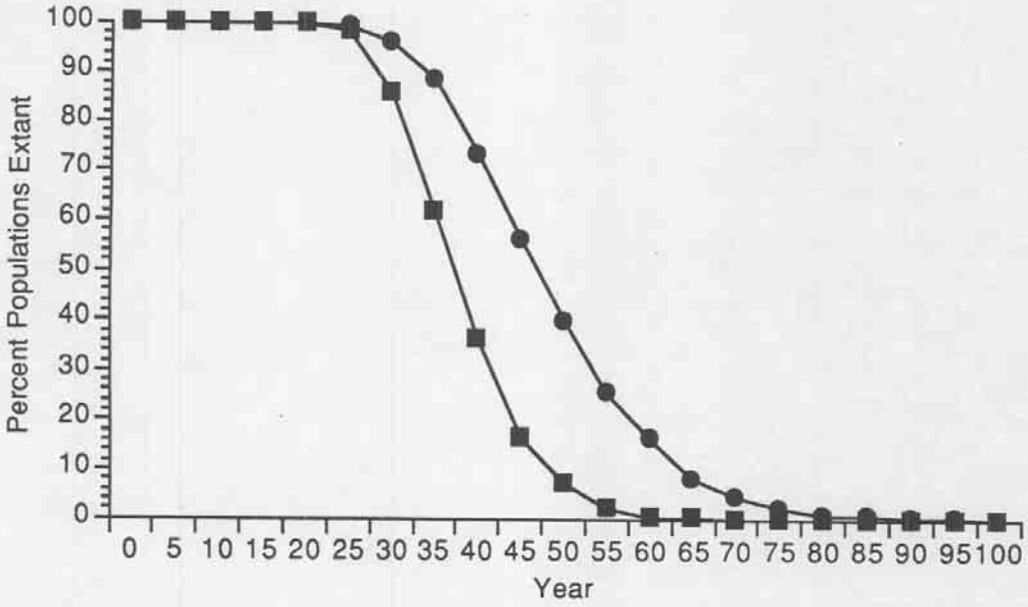


Figure 30. Extinction curve for the Californian population of Peregrine Falcons.




## RECOMMENDATIONS

> " In conclusion, a priority for future studies is some assessment of the degree of change in peregrine reproduction, age of first breeding, and survival of pre-breeders, as populations rise. Only then can the effects of reduced production or survival on breeding numbers be more accurately predicted." (Newton & Mearns 1988)

We endorse Newton and Mearns's call for deeper understanding of basic peregrine biology. The peregrines in the Midwest are particularly suited to the long-term type of research that will address questions of population regulation and

environmental and demographic stochasticity. As well as many behavioral and genetic hypotheses, the differential survival of adult males and females as well as questions regarding sex ratios could be easily pursued through this population. We recommend that every effort be made to continue monitoring this unique population for several reasons:

1) The numerous, city eyries in the Midwest are easily monitored and the young relatively easy to band,

2) The population's ten year history is well documented,

3) Important demographic information, particularly first year mortality and natural sex ratios are difficult to determine from small sample sizes,

4) The population is small enough to be substantially sampled,

5) Most of the population is banded and,

6) Public interest is high.

Population modeling should continue to be used as a tool for monitoring the progress of the Peregrine Population of the Upper Midwest. Demographic data should be updated annually as new information becomes available and new situations arise. At least two other populations of Peregrine Falcons have been modeled. The Californian population has been discussed above. The restored population on the west coast of Sweden has a history and size similar to that of the Midwestern U.S. population. Using VORTEX, the success of Projekt Pilgrimsfalk was modeled and gave rise to conclusions and recommendations that are similar to those we have endorsed for the Midwestern population (T. Ebenhard abstract to U. Seal). The predicted risk of extinction is close to 0% during the next 100 years for both the Midwest and Swedish populations. Further releases are unnecessary but will decrease the time to reach carrying capacity. Continued monitoring is recommended. The release projects in the Midwest and Sweden have both succeeded.

## ACKNOWLEDGMENTS

We are indebted to P. Redig for his leadership in restoring peregrines to the Midwest, for providing essential records, gathering information, and for his enthusiasm for this research. We are also truly grateful for the help provided by numerous biologists, and peregrine enthusiasts who have spent countless hours identifying and monitoring the peregrines in the Midwest. We appreciate discussions with R. Moen and T. Starfield as we explored modeling possibilities. Our gratitude also goes to U. Seal of the Species Survival Commission of IUCN, who has not only been a leader in the PVA process but has allowed us to benefit from his expertise. This research was made possible by the financial support of the U. S. Fish & Wildlife Service through M. Fuller and the U. S. Army through W. Seegar, The Minnesota Department of Natural Resources Non-game Program, the Graduate School of the University of Minnesota, and the Clayton Natural History Fund and the Wilke Natural History Fund of the Bell Museum of Natural History, University of Minnesota.

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**APPENDIX 1--List of peregrines sighted in the Midwest**

APPENDIX 1

| Stud # | ID | Sex | Hatch | Fledged | | Last Sighted | | Year | Gen | Sire | Dam | Comment | Subspecies |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1397 | 1X | m | 89 | Winnipeg | Man | Winnipeg | Man | 93 | B-3 | 2400 | 1171 | attempted breedi | 7a x t |
| 2404 | BH | f | 90 | Brandon | Man | Winnipeg | Man | 93 | B-1 | unk | unk | attempted breedi | a |
| 1481 | 56V | f | 90 | Madison | WI | St Louis | MO | 92 | B-1 | 114 | 115 | attempted breedi | b x pere |
| 1540 | 55R | f | 91 | Cincinnati | OH | Detroit2 | MI | 93 | B-1 | 32 | 33 | attempted breedi | a |
| 1583 | 28R | f | 91 | Des Moines | IA | Topeka | KA | 93 | B-1 | 7 | 82 | attempted breedi | peal |
| 1624 | 41X | m | 91 | Toledo | OH | Detroit1 | MI | 92 | B-2 | 1106 | 2402 | attempted breedi | a |
| | RED 1/2 | m | ? | Brandon | Man | Regina | Sask | 93 | B-1 | | | attempted breeding | |
| | unk-wild | m | ? | | | Bong | MN | 93 | B-2 | | | attempted breeding | |
| | Aurora | f | ? | | | Columbus | OH | 93 | B-1 | | | attempted breeding | |
| | Laser | m | ? | | | Columbus | OH | 93 | B-1 | | | attempted breeding | |
| | unk | m | ? | | | Topeka | KA | 93 | B-1 | | | attempted breeding | |
| 1009 | Billy ray | m | 83 | Weaver Dunes | MN | Multifoods | MN | 87 | B-1 | unk | unk | breeding | a |
| 1052 | Harriet | f | 85 | Multifoods | MN | Chicago | IL | 93 | B-1 | 116 | 117 | breeding | 3b x a |
| 1041 | Radar | m | 85 | Weaver Dunes | MN | NCL | MN | 89 | B-1 | unk | unk | breeding | a x peal |
| 2400 | RED 5P9 | m | 85 | | | Winnipeg | Man | 93 | B-1 | unk | unk | breeding | a |
| 1059 | Jingles | m | 86 | Chicago | IL | Chicago | IL | 93 | B-1 | 34 | 35 | breeding | a |
| 1061 | MF-1 | f | 86 | Multifoods | MN | Multifoods | MN | 93 | B-1 | 41 | 42 | breeding | a x t |
| 1065 | Cohan | m | 86 | Multifoods | MN | NCL | MN | 88 | B-1 | 36 | 37 | breeding | 2 b x t x pere |
| 1074 | 12R | f | 86 | Multifoods | MN | NCL | MN | 93 | B-1 | 24 | 25 | breeding | 2 peal x a x pere |
| 1094 | 43R | f | 86 | Multifoods | MN | Palisade Head | MN | 93 | B-1 | 32 | 33 | breeding | a |
| 1101 | Alfie | m | 86 | Multifoods | MN | Multifoods | MN | 88 | B-1 | unk | unk | breeding | a |
| 1095 | Beaner | m | 86 | Multifoods | MN | NCL | MN | 91 | B-1 | 32 | 33 | breeding | a |
| 2401 | 6P3 | m | 86 | quebec | Queb | Bong/ Blatnik | MN | 93 | B-1 | unk | unk | breeding | a |
| 1096 | Larry | m | 86 | Tofte | MN | Palisade Head | MN | 90 | B-1 | unk | unk | breeding | a |
| 1164 | 08P | f | 87 | Chicago | IL | East Chicago | IN | 91 | B-1 | 1 | 2 | breeding | b |
| 1127 | 03Y | m | 87 | ft s | | Milwaukee | WI | 91 | B-1 | 3 | 4 | breeding | 3 peal x pere |
| 1106 | 20Y | m | 87 | Grand Rapids | MI | Detroit1/Toled | MI/OH | 93 | B-1 | 34 | 35 | breeding | a |
| 1102 | 05P | f | 87 | Mayo | MN | Milwaukee | WI | 88 | B-1 | 34 | 35 | breeding | a |
| 1132 | 04Y | m | 87 | Mayo | MN | Multifoods | MN | 93 | B-1 | 10 | 9 | breeding | b x peal |
| 1149 | 34Y | m | 87 | Milwaukee | WI | East Chicago | IN | 91 | B-1 | 24 | 25 | breeding | 2 peal x pere x a |
| 1171 | 27P | f | 87 | Multifoods | MN | Winnipeg | Man | 91 | B-2 | 1009 | 1061 | breeding | 3 a x t |
| 1143 | 20P | f | 87 | Rouchleau Pi | MN | ELC etc. | MN | 93 | B-1 | 43 | 44 | breeding | peal x pere |
| 2402 | 3C7 | f | 87 | | Ont | Toledo | OH | 93 | B-1 | unk | unk | breeding | a |
| 1209 | 52P | f | 88 | Grand Rapids | MI | Gary | IN | 93 | B-1 | 5 | 9 | breeding | 3 peal x a |
| 1210 | 55Y | m | 88 | Grand Rapids | MI | Gary | IN | 92 | B-1 | 5 | 9 | breeding | 3 peal x a |

APPENDIX 1

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1254 | 20V | f | 88 | Isle Royale | MI | Milwaukee | WI | 93 | B-1 | 60 | 61 | breeding | 3 a xpeal |
| 1186 | 05T | m | 88 | Mayo | MN | Wards | MN | 93 | B-1 | 34 | 35 | breeding | a |
| 1214 | 08V | f | 88 | Mayo | MN | Control Data | MN | 91 | B-1 | 20 | 21 | breeding | a x peal |
| 1258 | 04T | m | 88 | Mayo | MN | Control Data/ | MN | 93 | B-1 | 22 | 46 | breeding | a x b |
| 1187 | 06T | m | 88 | Mayo | MN | Rochester | MN | 93 | B-1 | 34 | 35 | breeding | a |
| 1268 | 13T | m | 88 | Multifoods | MN | Bayport | MN | 92 | B-2 | 1101 | 1061 | breeding | 3 a x t |
| 1175 | 34R | f | 88 | Multifoods | MN | Bong | MN | 93 | B-1 | 34 | 35 | breeding | a |
| 1194 | 11V | f | 88 | Rouchleau Pi | MN | Wards | MN | 93 | B-1 | 23 | 9 | breeding | a x peal |
| 1515 | 67Z | m | 88 | Toledo | OH | Cleveland | OH | 93 | B-2 | unk | 2402 | breeding | a x unk |
| 1300 | 52V | f | 89 | Cedar Rapids | IA | Winnipeg | Man | 93 | B-1 | 43 | 44 | breeding | peal x pere |
| 1319 | 42V | f | 89 | Chicago | IL | Sheboygan | WI | 93 | B-1 | 23 | 81 | breeding | a x peal |
| 1304 | 25V | f | 89 | ELC | MN | Rouchleau Pit | MN | 93 | B-1 | 3 | 4 | breeding | 3 peal x pere |
| 1387 | 31V | f | 89 | Multifoods | MN | Bayport | MN | 93 | B-2 | 1132 | 1061 | breeding | a x b x peal x t |
| 1384 | 31T | m | 89 | NCL | MN | Colonnade | MN | 93 | B-2 | 1041 | 1074 | breeding | 4 peal x 3 a x pere |
| 1353 | 53T | m | 89 | Omaha | NE | Omaha | NE | 93 | B-1 | 53 | 29 | breeding | a |
| | unk | m | 89 | St. Louis | MO | St Louis | MO | 93 | B-1 | | | breeding | |
| 1419 | 94T | m | 90 | Cedar Rapids | IA | Becker | MN | 93 | B-1 | 28,49.7 | 14 | breeding | a x unk |
| 1445 | 93t | m | 90 | Cedar Rapids | IA | St Louis | MO | 93 | B-1 | 104 | 105 | breeding | 3 peal x a |
| 1466 | 81V | f | 90 | Cedar Rapids | IA | Colonnade | MN | 93 | B-1 | 20 | 100 | breeding | a x peal |
| 1467 | 20X | m | 90 | Cedar Rapids | IA | Des Moines | IA | 93 | B-1 | 106 | 107 | breeding | 11 peal x 5 a |
| 1456 | 21X | m | 90 | Cincinnati | OH | Dayton | OH | 93 | B-1 | 5 | 81 | breeding | 3 peal x a |
| 1493 | 75V | f | 90 | Control Data | MN | Rochester | MN | 93 | B-2 | 1258 | 1214 | breeding | 2 a x b x peal |
| 1401 | 74T | m | 90 | Madison | WI | Milwaukee | WI | 93 | B-1 | 36 | 37 | breeding | 2 b x pere x t |
| 1402 | 72T | m | 90 | Madison | WI | Madison | WI | 92 | B-1 | 36 | 37 | breeding | 2 b x t x pere |
| 1407 | 79T | m | 90 | Madison | WI | Gary | IN | 93 | B-1 | 36 | 37 | breeding | 2 b x pere x t |
| 1479 | 70T | m | 90 | Madison | WI | Sheboygan | WI | 93 | B-1 | 112 | 113 | breeding | peal x pere |
| 1480 | 57V | f | 90 | Madison | WI | East Chicago | IN | 93 | B-1 | 1 | 111 | breeding | a x b |
| | unk | f | 90 | St. Louis | MO | St Louis | MO | 93 | B-1 | | | breeding | |
| 2403 | RED AD | f | 90 | Sudbury | Ont | Detroit1 | MI | 93 | B-1 | unk | unk | breeding | a |
| 1512 | BLACK 3D | m | 90 | Winnipeg | Man | Regina | Sask | 93 | B-3 | 2400 | 1171 | breeding | 7a x t |
| 2405 | RED 8B3 | f | 90 | Winnipeg | Man | Regina | Sask | 93 | B-1 | unk | unk | breeding | a |
| 1519 | 66R | f | 91 | Columbus | OH | Dayton | OH | 93 | B-1 | 106 | 107 | breeding | 11 peal x 5 a |
| 1589 | 33R | f | 91 | Des Moines | IA | Omaha | NE | 93 | B-1 | 24 | 25 | breeding | 2 peal x a x pere |
| 1550 | 49R | f | 91 | Des Moines | IA | Cedar Rapids | IA | 93 | B-1 | | | breeding | peal |
| 1597 | 57R | f | 91 | Indianapolis | IN | Cincinnati | OH | 93 | B-1 | 110 | 103 | breeding | peal |
| 1584 | 71X | m | 91 | Isle Royale | MI | Palisade Head | MN | 93 | B-1 | 110 | 103 | breeding | peal |

APPENDIX 1

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1605 | 13R | f | 91 | Kansas City | MO | Des Moines | IA | 93 | B-1 | 1 | 111 | breeding | a x b |
| 1612 | 36R | f | 91 | Lacrosse | WI | Becker | MN | 93 | B-1 | 123 | 2 | breeding | a x b |
| 1626 | 25R | f | 91 | Multifoods | MN | Madison | WI | 92 | B-2 | 1132 | 1061 | breeding | a x b x peal x t |
| | X/H | f | 91 | Nipigon | Ont | Cohasset | MN | 93 | B-1 | | | breeding | |
| 1638 | 74X | m | 91 | Rouchleau Pi | MN | Cohasset | MN | 93 | B-2 | | 1304 | breeding | 3 peal x pere x 4u |
| 1630 | 55X | m | 91 | Wards | MN | Blackdog | MN | 93 | B-2 | 1186 | 1194 | breeding | 3a x peal |
| | ?8P | m | 91 | | | Detroit1 | MI | 92 | B-1 | | | breeding | |
| | pop | m | 91 | | | Detroit1 & 2 | MI | 93 | B-1 | | | breeding | |
| 1818 | 51Z | m | 92 | Bayport | MN | Bayport | MN | 93 | B-3 | | 1387 | breeding | 4a x2t x b x peal |
| 1815 | 23W | f | 92 | Omaha | NE | Cleveland | OH | 93 | B-2 | 1353 | 1589 | breeding | 5a x 2 peal x pere |
| | 58? | m | 88/89 | | | East Chicago | IN | 93 | B-1 | | | breeding | |
| | unk | f | ? | 5th year | | Trap Hills | MI | 93 | B-1 | unk | unk | breeding | |
| | unk | m | ? | 5th year | | Trap Hills | MI | 93 | B-1 | unk | unk | breeding | |
| | unbanded | f | ? | ? | | Blackdog | MN | 93 | B-2 | | | breeding | |
| 1708 | .2/3 | f | ? | Muscatine | IA | St Louis | MO | 93 | B-1 | 159 | 160 | breeding | a |
| | unk | m | ? | | | Cedar Rapids | IA | 93 | B-1 | unk | unk | breeding | |
| | unk | m | ? | | | Cincinnati | OH | 93 | B-1 | unk | unk | breeding | |
| | green ban | m | ? | | | ELC etc. | MN | 93 | B-1 | | | breeding | |
| | unk | m | adult | 2nd year | | Pie Island | Ont | 93 | B | | | breeding | |
| | unk | f | adult | 2nd year | | Pie Island | Ont | 93 | B | | | breeding | |
| | unk | m | adult | 3rd year | | Nipigon River | Ont | 93 | B | | | breeding | |
| | unk | f | adult | 3rd year | | Nipigon River | Ont | 93 | B | | | breeding | |
| | unk | m | adult | 3rd year | | Sibley Pennin | Ont | 93 | B | | | breeding | |
| | unk | f | adult | 3rd year | | Sibley Pennin | Ont | 93 | B | | | breeding | |
| | unk | m | adult | 4th year | | Porcupine Mt. | MI | 93 | B | | | breeding | |
| | unk | f | adult | 4th year | | Porcupine Mt. | MI | 93 | B | | | breeding | |
| | unk | m | adult | | | Lake Superior | Ont | 93 | B | | | breeding | |
| | unk | f | adult | | | Lake Superior | Ont | 93 | B | | | breeding | |
| | unk | m | adult | | | Mt. McKay | Ont | 93 | B | | | breeding | |
| | unk | f | adult | | | Mt. McKay | Ont | 93 | B | | | breeding | |
| 1580 | 21R | f | 91 | | | | | 92 | A-1 | 7 | 82 | broken leg | peal |
| 1389 | 86Y | m | 89 | Chicago | IL | louis | | 91 | A-2 | 1059 | 1052 | crippled | a x unk |
| 1314 | 57T | m | 89 | Omaha | NE | | | 91 | A-2 | | | dead | |
| 1124 | 18Y | m | 87 | Grand Rapids | MI | Ann Arbor | MI | 89 | A-2 | 3 | 4 | found dead | 3 peal x pere |
| 1110 | 01P | f | 87 | Rochester | MN | | OH | 88 | A-1 | 36 | 37 | found dead | 2 b x t x pere |
| 1022 | 877-42442 | f | 84 | Weaver Dunes | MN | Devil's Lake | WI | 87 | a-3 | unk | unk | paired | a |

APPENDIX 1

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1070 | 576-87052 | m | 86 | Chicago | IL | Chicago | IL | 88 | A-3 | unk | unk | paired | peal |
| 1123 | 11P | f | 87 | Chicago | IL | Hastings | MN | 88 | A-1 | 36 | 37 | paired | 2 b x t x pere |
| 1166 | 14Y | m | 87 | Chicago | IL | Chicago | IL | 91 | A-4 | unk | unk | paired | a |
| 1139 | Bogey | f | 87 | Detroit | MI | | OH | 90 | A-3 | 5 | 9 | paired | 3 peal x a |
| 1168 | Zoar | f | 87 | Milwaukee | WI | Chicago | IL | 90 | A-3 | unk | unk | paired | a |
| 1429 | 76V | f | 90 | Isle Royale | MI | Duluth | MN | 92 | A-2 | 43 | 44 | paired | peal x pere |
| 1604 | 2206-1385 | m | 91 | Des Moines | IA | | | 92 | A-1 | 123 | 2 | paired | |
| 1501 | 85V | f | 92 | Rouchleau Pi | MN | Blatnik | MN | 93 | WB1 | unk | 1304 | paired | |
| | wild-unk | m | 92 | | | Chicago (Hyde | IL | 93 | WB | | | paired | |
| | unk | f | ? | | | Chicago (Hyde | IL | 93 | | | | paired | |
| | hybrid | | ? | | | Cleveland | OH | 92 | D | unk | unk | paired | hybrid |
| | unk | f | ? | | | Cleveland (Me | OH | 93 | | | | paired | |
| | unk | m | ? | | | Cleveland (Me | OH | 93 | | | | paired | |
| | unk | f | ? | | | Jefferson City | MO | 93 | | | | paired | |
| | unk | m | ? | | | Jefferson City | MO | 93 | | | | paired | |
| | unk | f | ? | | | Kansas City | MO | 93 | | | | paired | |
| | unk | m | ? | | | Kansas City | MO | 93 | | | | paired | |
| | unk | f | ? | | | Lincon | NE | 93 | | | | paired | |
| | unk | m | ? | | | Lincon | NE | 93 | | | | paired | |
| | unk | f | ? | | | Pictured Rocks | MI | 93 | | | | paired | |
| | unk | m | ? | | | Pictured Rocks | MI | 93 | | | | paired | |
| | unk | f | adult | | | Davenport | IA | 93 | | | | paired | |
| | unk | m | adult | | | Davenport | IA | 93 | D | | | paired | |
| 1029 | 877-42443 | f | 84 | Tofte | MN | Tofte | MN | 86 | A-2 | unk | unk | seen | a |
| 1060 | 816-21832 | m | 86 | Multifoods | MN | NCL | MN | 88 | A-3 | unk | 40 | seen | peal x unk |
| 1093 | Jaffray | m | 86 | Multifoods | MN | Rochester | MN | 87 | A-1 | 32 | 33 | seen | a |
| 1160 | 31Y | m | 87 | Isle Royale | MI | Isle Royale | MI | 88 | A-1 | unk | 17 | seen | a x unk |
| 1227 | 14V | f | 88 | Rouchleau Pi | MN | Multifoods | MN | 89 | A-1 | unk | unk | seen | a |
| 1242 | 41Y | m | 88 | Trap Hills | MI | Trap Hills | MI | 89 | A-1 | 22 | 2 | seen | a x b |
| 1411 | 84T | m | 90 | Bayport | MN | minn | | 91 | A-1 | 34 | 35 | seen | a |
| 1454 | 93V | f | 90 | Cedar Rapids | IA | NCL | MN | 91 | A-1 | 24 | 25 | seen | 2 peal x pere x a |
| 1428 | 83T | m | 90 | Isle Royale | MI | Isle Royale | MI | 91 | A-1 | 43 | 44 | seen | peal x pere |
| 1451 | 15X | m | 90 | Isle Royale | MI | Isle Royale | MI | 91 | A-1 | 5 | 83 | seen | 3 peal x a |
| 1488 | 72V | f | 90 | Multifoods | MN | St Cloud | MN | 91 | A-1 | 1132 | 1061 | seen | a x b x peal x t |
| | RED 5/1 | m | 91 | Sudbury | Onta | Detroit2 | MI | 93 | A-2 | | | seen | |
| 2406 | 3B1 | f | 84 | mont | | Detroit1 | MI | 92 | A-8 | unk | unk | territorial | a |

APPENDIX 1

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1349 | 48T | m | 89 | Madison | WI | Madison | WI | 93 | B-1 | 32 | 33 | territorial | a |
| 1639 | 31R | f | 91 | Rouchleau Pi | MN | Monticello | MN | 93 | B-2 | unk | 1304 | territorial | |
| 1776 | 78R | f | 92 | Multifoods | MN | Cohasset | MN | 93 | WB | 1132 | 1061 | territorial | |
| 1689 | C/M | m | 92 | Muscatine | IA | Muscatine | IA | 93 | | 34 | 35 | territorial | |
| | killed male | | ? | | | Des Moines | IA | 93 | A | | | territorial | |
| | unk | | ? | | | Fort Wayne | IN | 93 | | | | territorial | |
| | unk | | ? | | | Indianapolis | IN | 93 | | | | territorial | |
| | unk | | ? | | | Kenosha | WI | 93 | | | | territorial | |
| | unk | | ? | | | Racine | WI | 93 | | | | territorial | |

## APPENDIX 2--Number fledglings per site per year and the number of fledglings resighted

## APPENDIX 2

| Site | Fledglings | | | | | | | | | | | | Number survived for at least one year | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | total | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | total |
| Akron | | | | | | | | | | | 7 | 7 | | | | | | | | | | | 0 | 0 |
| Bayport | | | | | | | | | 2 | 3 | 3 | 8 | | | | | | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| Bong Bridge | | | | | | | | | | 2 | | 2 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BWCA | | | | | | | | | 3 | | | 3 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Cedar Rapids | | | | | | | | 9 | 13 | | | 22 | | | | | | | | 1 | 5 | | 0 | 6 |
| Chicago | | | | | 5 | 11 | 10 | 10 | 10 | | | 46 | | | | | 2 | 4 | 0 | 1 | 0 | | 0 | 7 |
| Chicago, IL | | | | | | | 2 | 1 | | | 3 | 6 | | | | | | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| Cincinnatti | | | | | | | | | 6 | 7 | | 13 | | | | | | | | | 1 | 1 | 0 | 2 |
| Collinade | | | | | | | | | | | 4 | 4 | | | | | | | | | | 0 | 0 | 0 |
| Columbus | | | | | | | | 5 | 8 | 7 | | 20 | | | | | | | | 0 | 0 | 1 | 0 | 1 |
| Control Data | | | | | | | | | 3 | 2 | | 5 | | | | | | | | | 1 | 0 | 0 | 1 |
| Des Moines | | | | | | | | | | 19 | | 19 | | | | | | | | | | 4 | 0 | 4 |
| Detroit | | | | | | 5 | 6 | | | | | 11 | | | | | | 1 | 0 | | | | 0 | 1 |
| Detroit | | | | | | | | | | | 2 | 2 | | | | | | | | | | | 0 | 0 |
| East Chicago, IL | | | | | | | | 3 | 2 | 1 | 4 | 10 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| ELC, MN | | | | | | | | | 2 | 3 | | 5 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Evanston | | | | | | | | 3 | | | | 3 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Fort Wayne | | | | | | | | | | | 18 | 18 | | | | | | | | | | | 0 | 0 |
| Grand Island | | | | | | | | | | | 8 | 8 | | | | | | | | | | | 0 | 0 |
| Grand Rapids | | | | | 5 | 6 | 7 | | | | | 18 | | | | | 0 | 2 | 2 | | | | 0 | 4 |
| Hill Annex | | | | | | | | 9 | | | | 9 | | | | | | | | 0 | 0 | | 0 | 0 |
| Indianapolis | | | | | | | | | | 15 | | 15 | | | | | | | | | | 1 | 0 | 1 |
| Isle Royale | | | | | | 5 | 5 | 10 | 18 | 12 | | 50 | | | | | | 1 | 1 | 0 | 3 | 1 | 0 | 6 |
| Kansas City | | | | | | | | | | 11 | 13 | 24 | | | | | | | | | | 1 | 0 | 1 |
| Kenosha | | | | | | | | | | | 15 | 15 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Lacrosse | | | | | | | | | | 15 | 14 | 29 | | | | | | | | | | 2 | 0 | 2 |
| Madison | | | | | | | 7 | 9 | 19 | | | 35 | | | | | | | 0 | 1 | 6 | | | 7 |
| Madison | | | | | | | | | | | 2 | 2 | | | | | | | | | | | 0 | 0 |
| Milwaukee | | | | | | 14 | | | | | | 14 | | | | | | 2 | 0 | 0 | | 0 | | 2 |
| Milwaukee, WI | | | | | | | 4 | 2 | 4 | 2 | 4 | 16 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Mt. Leveaux | | | | | | | | 1 | 3 | | | 4 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Multifoods | | | | 6 | 15 | | | | | | | 21 | | | | 1 | 8 | 0 | 0 | 0 | 0 | | | 9 |
| Multifoods, MN | | | | | | 3 | 4 | 4 | 4 | 3 | 4 | 22 | | | | | | 1 | 2 | 1 | 1 | 1 | 1 | 7 |

APPENDIX 2

| | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Muscatine | | | | | | | | | | | 8 | 8 | | | | | | | | | | | 2 | 2 |
| NCL, MN | | | | | | | 2 | 4 | 3 | 3 | 3 | 15 | | | | | | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| Nipigon | | | | | | | | | | 10 | 12 | 22 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Omaha | | | | | | | 7 | 11 | 4 | | | 22 | | | | | | | | 2 | 0 | 0 | 0 | 2 |
| omaha | | | | | | | | | | | 3 | 3 | | | | | | | | | | | 1 | 1 |
| Palisade Head, MN | | | | | | | 2 | 1 | 4 | 3 | 3 | 13 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Pictured Rocks | | | | | | | | 10 | | 12 | | 22 | | | | | | | | 0 | | 0 | 0 | 0 |
| Racine | | | | | | | | | | | 10 | 10 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| regina | | | | | | | | | | | 4 | 4 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Rochester | | | | | | 20 | 12 | | | | | 32 | | | | | | 3 | 4 | | | | 0 | 7 |
| Rochester | | | | | | | | | | | 2 | 2 | | | | | | | | | | | 0 | 0 |
| Rochleua | | | | | | | | | | 2 | 4 | 6 | | | | | | 0 | 0 | 0 | 0 | 2 | 1 | 3 |
| Rouchleau | | | | | | 5 | 12 | 11 | | | | 28 | | | | | | 1 | 2 | 0 | | | 0 | 3 |
| sheboygan | | | | | | | | | | | 2 | 2 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| sherco | | | | | | | | | | | 2 | 2 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| St. Louis | | | | | | | | | | 2 | | 2 | | | | | | | | | | 0 | 0 | 0 |
| Thunder Bay | | | | | | | | 16 | 10 | 10 | | 36 | | | | | | | | 0 | 0 | 0 | 0 | 0 |
| Tofte/ELC | | | 5 | 7 | 18 | | 10 | 9 | | | | 49 | | | 1 | 0 | 1 | | 0 | 1 | | | 0 | 3 |
| Toledo, OH | | | | | | | 2 | | 2 | 1 | 3 | 8 | | | | | | 0 | 1 | 0 | 0 | 1 | 0 | 2 |
| Trap Hills | | | | | | 4 | 10 | | | | | 14 | | | | | | 0 | 1 | | | | 0 | 1 |
| Trap Hills | | | | | | | | | | 1 | | 1 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| U. S. Steel, Gary, IN | | | | | | | | | 1 | 2 | 1 | 4 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Wards,St.Paul, MN | | | | | | | | | 2 | 4 | 4 | 10 | | | | | | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| Weaver Dunes | 5 | 10 | 11 | 12 | 3 | | | | | | | 41 | 0 | 1 | 1 | 1 | 0 | | | | | | 0 | 3 |
| Winnipeg, Manitoba | | | | | | | | 4 | 2 | 2 | 2 | 10 | | | | | | 0 | 0 | 1 | 1 | 0 | 0 | 2 |
| Winnipeg, Manitoba | | | | | | | | | | | 4 | 4 | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | | | | | | | | | | |
| TOTALS | 5 | 10 | 16 | 25 | 46 | 73 | ## | ## | ## | ## | ## | 856 | 0 | 1 | 2 | 2 | 11 | 15 | 13 | 10 | 18 | 16 | 6 | 94 |

**APPENDIX 3--Laboratory protocols**
**(on diskette, not included here)**

# APPENDIX 4--NCL paternity story

Figure 1. DNA fragments highlighted by the pMR1-4 probe. The patterns show that Maverick has more in common with the 1990 NCL chicks than Beaner does. Although Beaner and Maverick are first cousins, the DNA fragments inherited from their related parents are very different.

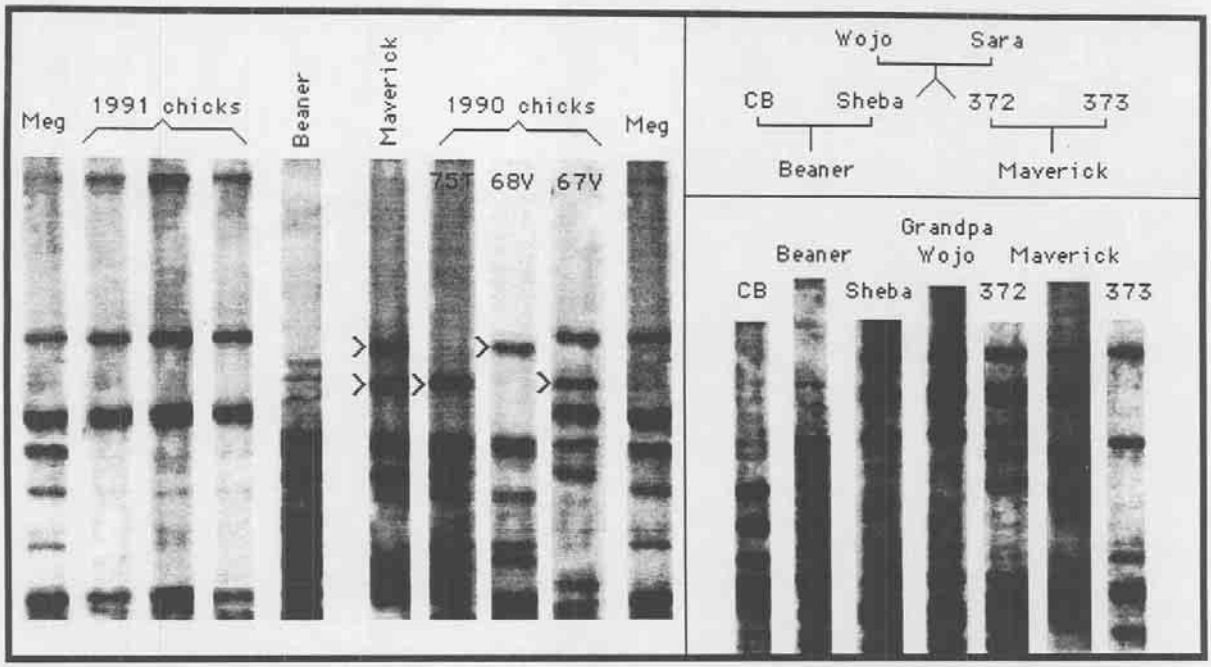
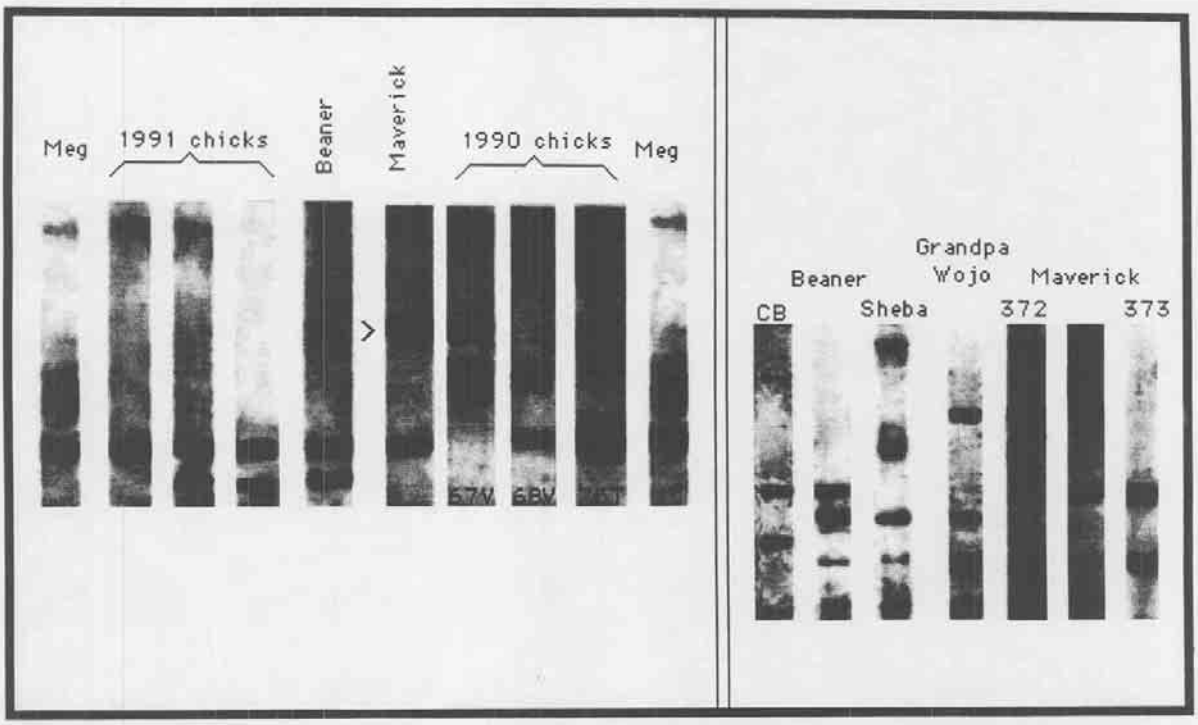


Figure 2. DNA fragments highlighted by the pVPϕ1-3 probe. The patterns show that at least one of the NCL chicks (67V) could be Maverick's but not Beaner's offspring. The band in question comes from Maverick's and Beaner's common ancestor, Wojo.



# PEREGRINE PATERNITY CASE

H.B.TORDOFF, S.M.MOEN, P.T.REDIG, J.L. LONGMIRE, D.N.FOSTER

Meg is the reigning peregrine of downtown St. Paul but she doesn't have much luck with the opposite sex. Cohan, who was released with Meg in Minneapolis and fathered her first young, departed in the fall of 1988 and never returned. Radar, an older male hacked at Weaver Dunes in 1983, moved into Meg's penthouse eyrie in spring 1989; he helped her raise their four young until he was killed by an airplane on nearby Holman Field in early July. Within eight hours of Radar's death, Beaner (another male hacked with Meg) moved in and drove her fledged young out of town. After establishing his presence, Beaner left town to winter in warmer climes. Upon his return, he found yet another male courting Meg.

The details of what went on in the early spring of 1990 are sketchy. There were fights in public. Neighbors and relatives were involved. There were babies of unknown paternity.

Though Meg sounds like a soap opera star, she is an important part of the effort to reestablish peregrines in the Midwest. She was hacked from the Multifoods Tower in Minneapolis in 1986 along with 15 other falcons, two of which (Cohan and Beaner) eventually became her mates. She moved to the North Central Life (NCL) Tower in downtown St. Paul in 1987 and has nested there since 1988, fledging 15 offspring through 1992.

We keep detailed records and observations of the individual peregrines in the new Midwestern population. These records help us to evaluate management efforts, establish a detailed history of the reintroduction effort, and monitor the population's fate. All released birds and almost all of the wild young are banded with field-readable bands so that we can see who survives, where they settle down, and who is mated to whom each year. Since 1990 blood samples have been taken from released birds and, where possible, wild produced young and their parents. We are using the blood samples to assess the genetic diversity of the new population

through DNA fingerprinting and RFLP (short for "restriction fragment length polymorphisms", although nobody asked) analysis. Fortunately, field observations and the availability of blood samples from all of the principal players in the 1990 North Central Life drama have allowed us to identify the genetic father of the North Central Life chicks.

DNA fingerprinting and RFLP analysis have become standard techniques for studying questions of paternity and maternity. Species ranging from whales (Amos et al. 1991) to shrews (Tegelstrom et al. 1991) have been successfully studied using these genetic methods. Recently, through DNA fingerprinting, researchers identified the sires of Whooping Crane (Grus americana) chicks produced by artificial insemination with pooled semen (Longmire et al. 1992). Such information is valuable for the genetic management of small populations.

Fingerprinting and RFLP analyses target different areas of chromosomes and different types of polymorphisms (Longmire et al. 1988 and 1991), thereby giving two mostly independent estimates of genetic variability within a population. Methods and probes that were developed at the Los Alamos National Laboratory for Peregrine Falcons are being used in studies of adult turnover and genetic diversity in Greenland (Lisa Clepper, pers. comm.), subspecies identification during migration (Longmire et al. 1991), and genetic diversity of the Midwestern peregrines (our work).

Our story began to unfold when field observations led Tordoff to speculate that the male helping Meg raise the 1990 NCL chicks was not their father. Meg spends her winters in St. Paul, dining on pigeons and an occasional duck; she was seen repeatedly in February 1990. Then, on March 4, an adult male with a black band on his left leg and a silver one on his right appeared in the nest box. This new male was seen again on March 7, 10, 12, 19, and April 4.

On April 9, there were three eggs in the nest box and two peregrines were locked in spectacular battles throughout the day. These aerial battles were seen by office workers on the 24th floor of the Mentor Tower and by window washers who passed over the nest box that day as they cleaned the east face of the NCL tower. At the time, we thought the mated peregrines

were redirecting their agitation over the window washers' intrusion. In retrospect, the battles of April 9th might have been between the black-banded male and the newly returned Beaner, who wore only a single faded gold band on his right leg. The next day, there were two adults on the territory, the window washers were elsewhere, and all seemed normal. On June 23, we trapped the NCL male for a blood sample and were surprised to catch Beaner, not the black-banded male present in early spring.

On May 3, Tom Shearen reported a pair of peregrines on the Montgomery Ward tower, just three miles west of the NCL tower. The Ward female had laid three eggs on a bare ledge. We put the eggs in a gravel tray and one chick hatched on June 9 after at least 36 days of incubation. Back at the NCL tower, the chicks had hatched on May 14. The events of the spring led Tordoff to propose that the male at the Ward tower, Maverick, was the ousted father of the NCL brood, and that Beaner had spent his summer raising chicks sired by Maverick.

Although partly speculative, the story is based on some solid evidence. First, Beaner obviously replaced a black-banded male at the NCL tower between April 4 and June 23. Second, Tordoff had made a detailed plumage sketch of the blackbanded NCL male on March 4. Third, we had blood samples from Beaner, Meg, Maverick, and the NCL and Ward chicks.

The plumage sketch made on March 4, 1990, at the NCL nest box fits Maverick in all details even today. On March 12, 1993, we identified him at the Ward tower from the 1990 NCL sketch, two weeks before we were able to read his band for confirmation. Peregrines vary individually in plumage about as much as people vary in appearance; rarely do two individuals resemble one another enough to cause confusion, if good photos or drawings are available.

DNA fingerprinting analysis also supports Tordoff's reconstruction of events. Assuming that the DNA fragments detected are inherited from parents and do not arise spontaneously, the three chicks raised on the NCL Tower in 1990 are clearly not Beaner's offspring (Figs. 1 and 2). Even though Beaner and Maverick are first cousins, they have unique banding patterns detected by both the pVPf1-3 and pMR1-4 probes.

The DNA fragments detected with the pMR1-4 (RFLP) probe show the relationship between Maverick, Beaner, and their offspring most clearly (Fig. 1). Two high molecular weight bands (not to be confused with leg bands) found in the DNA of the 1990 NCL brood could not have been inherited from Meg or Beaner. These bands match bands found in Maverick's DNA profile, however, suggesting that he is indeed the true father.

The DNA fingerprints made with the pVPf1-3 (DNA-fingerprinting) probe do not refute Maverick's paternity of the 1990 NCL chicks. At least one of the chicks inherited a band of DNA equal in size and intensity to Maverick's unique one (Fig. 2). The other chicks could have been attributed to either Beaner or Maverick, had no other information been available.

Judging by plumage sketches and the single gold band on his right leg, Beaner was probably the male sighted in Hastings in 1988 and again for a few days in 1989. Early in 1989, he was in Bayport and later, after the death of Radar in July, at the NCL tower. Supporting evidence comes from his spring arrival dates of April 21, 1988 and April 16, 1989 at the Hastings cliff, checked daily by Joanne Dempsey. If Beaner arrived in St. Paul on April 9, 1990, when the fights were seen, he could not have sired the 1990 NCL brood since three eggs were already laid and the fourth would have been fertilized and in the oviduct. Nevertheless, he raised the brood while their true father established a neighboring territory and raised two more chicks (one fostered).

The peregrine population in the Midwest is the product of captive peregrines from around the world. By nature, some are migratory, some are not. Differences in behavior, morphology, and physiology, as well as luck, will make some individuals more successful than others in leaving their genes in the new population. In Beaner's case, his misfortune in 1990 was poor migratory timing. Arriving after Meg had already been inseminated cost him a breeding season and the energy required to raise four chicks that were not his. Natural selection acting on the generations to come should sort out the peregrines best adapted to life in the Midwest in the 21st century.

As an update, Meg continues to go through mates. After Beaner raised the 1990 brood, even though they were not his (we assume he was unaware of this), he left for the winter. Beaner returned in 1991 and, at age five, finally raised the first brood of his own, with Meg. He never returned for the 1992 season and he was replaced by Spanky, a new male, who had nested on the Control Data headquarters in Bloomington in 1990 and 1991 but raised three chicks with Meg in 1992.

We appreciate financial support from the U.S. Fish and Wildlife Service through M. Fuller, the U.S. Army through W. Seegar, the Minnesota Department of Natural Resources Nongame Wildlife Program, the Graduate School of the University of Minnesota, and the Dayton Natural History Fund and the Wilkie Fund for Natural History of the Bell Museum at the University. We also thank J.L. Longmire for teaching S. Moen the genetic techniques used in this study and for helpful advice.

Bell Museum of Natural History (HBT and SMM), The Raptor Center (PTR), Dept. of Animal Science (DF), University of Minnesota.

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**APPENDIX 5--Standard input**
**(on diskette, not included here)**