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Source: Journal of Raptor Research, 40(4) : 270-276

Published By: Raptor Research Foundation

URL: https://doi.org/10.3356/0892-1016(2006)40[270:EAGOAI]2.0.CO;2

J. Raptor Res. 40(4):270–276

ECOLOGY AND GENETICS OF AN ISOLATED POPULATION OF SWAINSON'S HAWKS IN ILLINOIS

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Abstract.—Swainson's Hawks (*Buteo swainsoni*) are listed as state-endangered in Illinois but virtually nothing is known about the small population persisting in the northeastern corner of the state. This population is separated from the nearest western populations by about 355 km. We estimated the size of the Illinois population at 10–16 adults in 2003 and conducted a preliminary study of the genetic relationship between the Illinois population and birds from Idaho near the western edge of their geographic range. We found slight but significant differentiation between the two populations. Band-sharing was high within (80–85%) and between (81%) populations suggesting fairly recent (within 150 yrs) isolation of the Illinois population.

Key Words: *Swainson's Hawk*; Buteo swainsoni; *isolated population*; *RAPD.*

ECOLOGíA Y GENÉTICA DE UNA POBLACIÓN AISLADA DE *BUTEO SWAINSONI* EN ILLINOIS

Resumen.—La especie *Buteo swainsoni* está catalogada como amenazada en el estado de Illinois, pero no se conoce prácticamente nada sobre una pequeña población que persiste en el extremo nororiental del estado. Esta población está separada de las poblaciones occidentales más cercanas por aproximadamente 355 km. Estimamos el tamaño de la población de Illinois en 10–16 adultos en 2003 y realizamos un estudio preliminar de las relaciones genéticas entre la población de Illinois y las aves de Idaho ubicadas cerca del extremo occidental de su rango de distribución. Encontramos diferencias pequeñas pero significativas entre las dos poblaciones. El porcentaje de bandas compartidas fue alto tanto dentro (80–85%) como entre (81%) poblaciones, lo que sugiere que la población de Illinois se aisló recientemente, en los últimos 150 años.

[Traducción del equipo editorial]

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The core breeding range of the Swainson's Hawk (*Buteo swainsoni*) extends from Iowa and Minnesota west to eastern Washington and from central Alberta south to northern Mexico. Small isolated populations occur in British Columbia, central California, and in northeastern Illinois. The Illinois population is restricted to Kane and McHenry counties west-northwest of the Chicago metropolitan area (Fig. 1). This population likely has been isolated from the western populations for over 100 yr (England et al. 1997). Although Swainson's Hawks are fairly common over much of their range, they have apparently always been rare in Illinois (Ridgway 1889, Cory 1909, Bohlen and Zimmerman 1989). First published records of Swainson's Hawks in northeastern Illinois were from Winnebago County (Prentice 1949). In the early 1970s nests were found in Kane County (Keir and Wilde 1976). Since then nests have been reported every year, with most in northern Kane County and fewer in southern McHenry County (Wenny et al. 2005).

Nest records indicate a small but stable population in a fairly small area (240 km^2, Table 1). Some of these nest sites have been used more than once over this 25-yr period. In Iowa, Swainson's Hawks occur mainly in the western and north-central parts of the state (Jackson et al. 1996). The nearest (and only) confirmed nest sites found during the Iowa Breeding Bird Atlas surveys of 1985–1990 are in Blackhawk and Cerro Gordo counties (Jackson et al. 1996), approximately 355 km from the Illinois nests. Swainson's Hawks nest regularly in western and southern Minnesota (Janssen 1987) but not in Wisconsin (Cory 1909, Robbins 1991).

In western North America, Swainson's Hawks forage most often in grasslands (including pastures, hay fields, and wheat), savanna, and open shrublands; they typically nest in trees in savanna, narrow riparian areas, or planted shelterbelts (England et al. 1997). In Illinois, they nest in oak savanna and woodland fragments embedded in an agricultural matrix. Residential and commercial development is rapidly increasing in the area near the nest sites (CRBC 1999), making habitat loss a threat to the survival of the Illinois population.

The Illinois Swainson's Hawks may represent the eastern limit of a population that was continuous across the west in pre-settlement times, or it may have always been isolated from the western populations. Available historical records are not detailed enough to address this question. Genetic studies, however, may shed light on the degree of genetic isolation and the length of time the Illinois birds have been isolated from the western birds. In addition, small populations are more susceptible to genetic drift and inbreeding, which often lead to declining genetic variability that in turn may affect population viability (e.g., Heschel and Paige 1995). However, low genetic variation may also result from a small founder population, and may or may not affect viability or divergence (Bollmer et al. 2005).

Our objectives in this study were to locate and monitor Swainson's Hawk breeding sites in northeastern Illinois, and to conduct a preliminary genetic comparison between the Illinois birds and a western population. We used these data to estimate the viability and potential divergence of the Illinois population.

METHODS

Nest Surveys. We searched for nests mainly in Kane and McHenry counties where hawk nests had been found in recent years. Additional nests were found by observing Swainson's Hawks in flight and searching in woodlots where they perched or near where they were observed repeatedly. After a nest was discovered, we monitored it weekly from the ground using binoculars or a spotting scope. About 2 wk prior to fledging, we climbed nest trees to band nestlings and take blood samples.

Genetic Sampling. We collected blood samples from five nestlings from five different nests. One sample was collected in 2002 and four were collected in 2003. The nest location sampled in 2002 was not used in 2003; thus, although birds were not individually marked, the samples likely represented five different breeding pairs. Because of the small population size, we could not be certain that the birds were unrelated. We also obtained blood samples from 15 birds near Middleton, Idaho, from the Conservation Research Foundation. These samples represented 14 nests: one individual from each of 13 nests (11 nestlings and two adults) and both adults from one nest. All blood samples were stored in approximately 1 ml of Queen's Lysis Buffer prior to genomic DNA extraction. We compared levels of genetic variation between Illinois and Idaho populations using random amplified polymorphic DNA markers (RAPDs). RAPD markers are short (10 base pair) primers that amplify specific portions of the DNA when two primers on opposite strands of the DNA molecule are located within 1500 or fewer base pairs; RAPDs have been used for evaluating population genetic structure (genetic differences among populations indicative of isolation and differentiation) and genetic diversity in other studies (Zwartjes 1999, Parker et al. 2002, Matics et al. 2005).

Each RAPD reaction contained 20 ng of DNA, PCR Buffer (20 mM Tris-HCL, 50 mM KCL), 0.2 μM of an Operon 10-base primer (from kits A and B; Operon Technologies), 1.5 mM $MgCl_2$, 0.1 mM each deoxyribonucleotide triphosphate (dNTP), 0.5 units of *Taq* polymerase, and sterile water (Sigma supplies) to a final volume of 25 μl. The PCR buffer, primer, $MgCl_2$, DNA, and water were com-

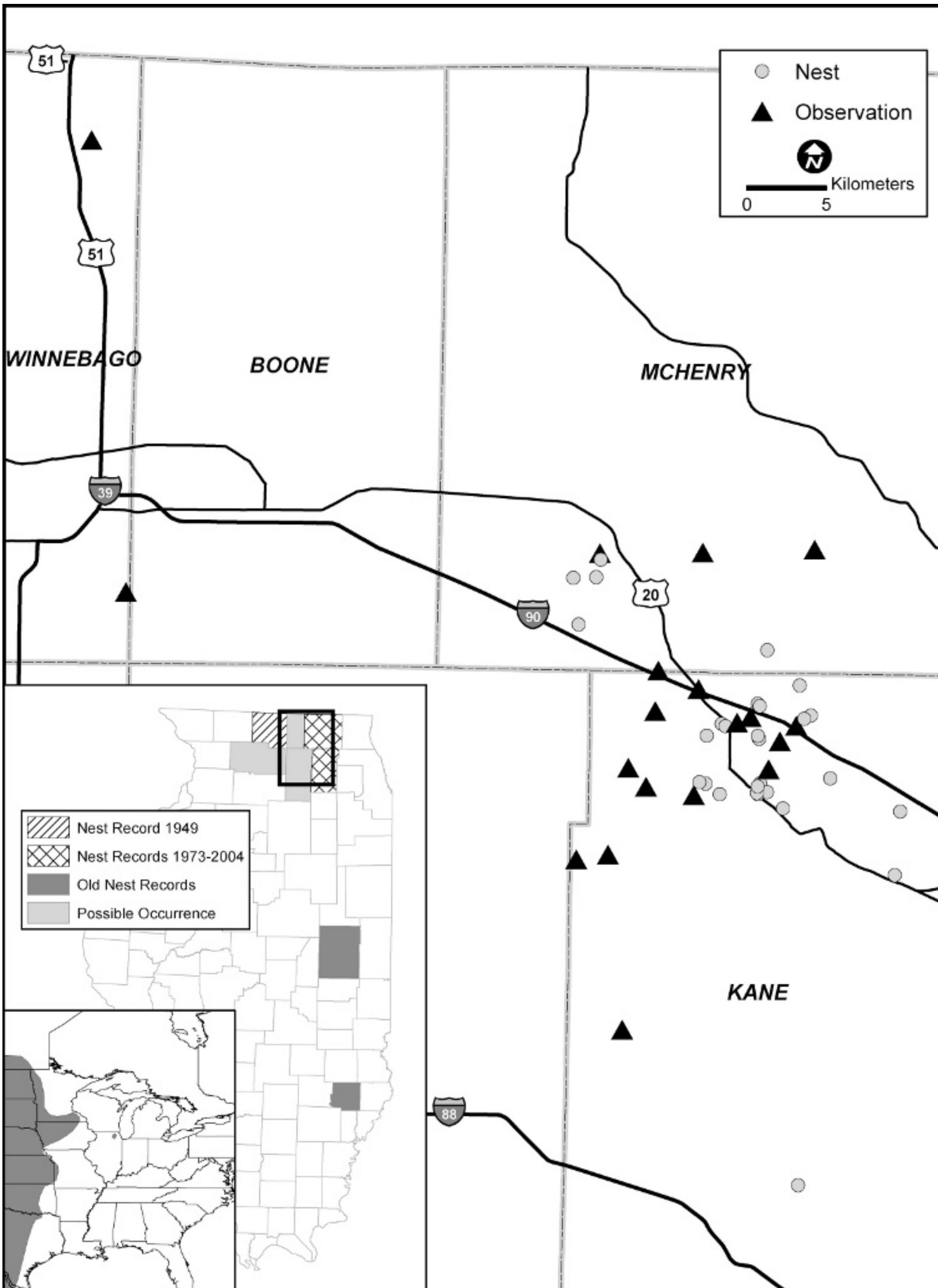

Figure 1. Approximate geographic range of Swainson's Hawk in the Midwest (from Peterson and Peterson 2002), historic and possible occurrences in Illinois counties (from Bohlen and Zimmerman 1989), and recent nest locations.

Table 1. Townships with nest records or breeding season observations of Swainson's Hawks 1973–2004. Data from this study, Illinois Department of Natural Resources, Natural Heritage Database, and published sources (Keir and Wilde 1976, Kleen et al. 2004, Morgan and Morgan 2005). Multiple observations in same area and year were considered as one observation. Reuse of a nest in successive years was tallied as one nest.

LOCATION COUNTY, TOWNSHIP	TYPE OF RECORD NEST	OBSERVATION
Kane County		
Blackberry	2	
Burlington		1
Dundee	1	
Elgin	1	
Hampshire	3	
Plato		1
Rutland	13	
Virgil		1
McHenry County		
Coral	2	
Grafton	1	
Riley	1	
Winnebago County		
Cherry Valley		1
Roscoe		2

bined to a volume of 15 μl. This mixture was then placed in a polycarbonate v-bottom microplate (MJ Research) and capped with 10 μl of liquid wax and subjected to a ''hot start'' (Chou et al. 1992) at 85°C. Following the hot start, *Taq* polymerase, dNTPs, and water were added to each sample bringing the final volume to 25 μl. The samples were then subjected to the following RAPD PCR profile: (1) 3 minutes at 94°C; (2) 30 seconds at 94°C; (3) 30 seconds at 36°C; (4) 1.5 minutes at 72°C; and (5) 10 minutes at 75°C (Williams et al. 1990). Steps 2 through 4 were repeated 44 times. Samples were run on an MJ Research PTC 100 thermal cycler. Each reaction was then run on a 1% agarose gel for 1.5 hours at 60 V. Gels were stained with ethidium bromide, visualized and photographed under UV light for scoring. Negative control reactions that contained no DNA were also used with every run in order to check for possible contamination or primer dimers.

We screened 40 primers from Operon Kits A and B for assessing genetic variation. From these forty primers, thirty-five produced clear, bright bands and were used to assess patterns of genetic variation within and among populations. We used both polymorphic and fixed bands from the 35 primers that produced clear banding patterns. Doing so gives a clear depiction of inbreeding at the whole genome level. Repeatability between PCR runs was assessed by comparing the same DNA samples used to first screen RAPD primers with those used in runs containing all DNA samples. Results showed that RAPD patterns were identical between runs.

Genetic Analysis. RAPD polymorphisms were analyzed under the following assumptions: (1) bands from different loci do not comigrate, (2) each locus is a two allele system in which only one allele is amplifiable, and (3) alleles arise from identical mutations among individuals (Black 1993, Lynch and Milligan 1994, Apostol et al. 1996). Levels of within- and between-population genetic variation were assessed by calculating the number of unique bands, mean percent band sharing, and levels of genetic differentiation. A band was considered unique only if it was detected within a single population. Percent band sharing was calculated using the following equation:

$$\text{Percent Band Sharing} = 2N_{AB}/(N_A + N_B) \times 100$$

where N_{AB} represents the number of bands that individuals A and B have in common. N_A and N_B are the total number of bands scored for each individual, respectively (Wetton et al. 1987). Percent band-sharing data were analyzed using ANOVA. Differences between means were evaluated using a Least Significant Difference (LSD) test. Genetic differentiation between the Idaho and Illinois populations was assessed using MANTEL-STRUCT (Miller 1999, Parker et al. 2002).

In addition, Wright's Fst (the fixation index, which is the reduction in heterozygosity of a subpopulation due to random genetic drift) was calculated from 120 RAPD fragments (loci) using the program RAPDFST 4.0.1 (Apostol et al. 1996). A contingency chi-square value was estimated to test Fst = 0. Fst was used in the following equation to estimate the effective migration rate: Nm = (1-Fst)/(4Fst) (Wright 1931). The effective migration rate (Nm) is an estimate of gene flow.

RESULTS

We found five Swainson's Hawk nests in 2003: three in northwestern Kane County and two in southwest McHenry County. Hawks were seen several times in three additional areas but no other nests were found. Thus, we estimated the 2003 population in the area we surveyed was approximately 10–16 adults. Of the five known breeding attempts in 2003, one failed during the egg stage, two failed during the nestling stage, and two produced a total of three fledglings. None of the 2003 nests were reused in 2004. We observed hawks throughout the same area of Kane and McHenry counties and found three new nests. We were not able to monitor these nests long enough to estimate success (but see Morgan and Morgan 2005).

Band-sharing was high within both the Illinois (80.6 ± 0.02%; mean ± 1 SD) and Idaho (85.8 ± 0.02%) populations. On average, 81.2 ± 0.02% of all bands were shared between the Illinois and Idaho populations.

Despite high levels of genetic similarity among individuals from these two sites, we still detected differences in population genetic structure. Individuals within the Idaho population were more similar to each other than to individuals within the Illinois population (ANOVA, $P < 0.05$). Individuals within these two populations were also found to be significantly more similar than individuals between these two populations (Mantel test; $P = 0.005$), indicating some differentiation of these two populations. F-statistics also indicated significant population genetic structure ($F_{st} = 0.092 \pm 0.013$, $P < 0.001$) despite a reasonably high Nm of 2.47 migrants per generation. In addition, among 120 fragments generated within the two populations, six were unique to the Idaho population and absent from the Illinois population, although not all individuals within the Idaho population carried the unique fragments.

DISCUSSION

The amount of band sharing within and between the Idaho and Illinois populations was relatively high. Similar analyses using RAPDs found only 49–54% band-sharing between isolated populations of scarlet gilia, *Ipomopsis aggregata* that did not interbreed (Paige and Heschel 1996).

A high level of band-sharing between populations is indicative of inbred populations with low levels of genetic variation. Such measures may result from either small effective populations, or bottleneck events that have purged much of the genetic variation (Wright 1931, 1969, Nei et al. 1975). The high levels of band-sharing between the Illinois and Idaho populations (81.2%), the low Fst value (0.092), and reasonably high migration rate (Nm = 2.47 migrants per generation) were somewhat surprising given the geographic isolation of the Illinois birds and the fact that Idaho birds were from the western limit of the Swainson's Hawk range, approximately 2400 km distant. One possible explanation is that the separation was a relatively recent event and the apparent genetic similarity we measured reflected shared ancestry. For example, populations that currently have no gene flow (i.e., interbreeding) at all but a shared ancestry can have an Fst less than 1 that could erroneously imply gene flow (Templeton et al. 1995). In spite of high genetic levels of band-sharing and reasonably high levels of gene flow (Nm = 2.47), we did uncover between-population genetic structure (via a Mantel test, an Fst, and several RAPD bands unique to Idaho), suggesting more limited gene flow than apparently measured.

These patterns of genetic variation are consistent with the breeding biology and migratory patterns of Swainson's Hawks. Swainson's Hawks are monogamous and, as in many other species of raptors, a breeding pair will typically stay together and return to the same breeding area as long as both survive. In central California, some pairs have remained together for at least 9 yr (Estep 1989, cited in England et al. 1997). Some individual hawks have survived for at least 24 yr, (B. Woodbridge unpubl. data, cited in Houston 2005) although a maximum lifespan of 15–20 yr may be more typical (Houston 2005). These studies demonstrate the potential for long-term monogamy.

Although most of the population in Illinois was not marked, circumstantial evidence indicated philopatry. First, the occasional reuse of nests from one year to the next suggested a mated pair, or at least one individual of a mated pair, returning to the same breeding site. Second, the concentrated pattern of nests in Illinois (Fig 1.) suggested strong philopatry. Third, we banded the three nestlings in 2003 and had one report of a banded immature bird in 2004. Finally, dispersal distances recorded in the west are much lower than the distance between Illinois and Iowa breeding sites (about 350 km). Natal dispersal distances averaged 8.2 km (range = 0–18.1 km) in California (Woodbridge et al. 1995) and 67 km (range 0–310 km) in Saskatchewan and Alberta (Houston 2005). Thus, philopatry and short natal dispersal distances may contribute to inbreeding.

Many Swainson's Hawks migrate overland through Central America, funnel through one or two mountain passes over the Andes mountain range in Colombia and spend the nonbreeding months in the grassland region (pampas) of northern Argentina and adjacent parts of Uruguay and Paraguay (England et al. 1997). The concentration of birds during the nonbreeding season presents the opportunity for mixing of breeding populations. For example, Bollmer et al. (2005) found 37% band-sharing (using minisatellite DNA markers rather than RAPDs) among eight wintering Swainson's Hawks, which suggested that birds from multiple breeding locations were represented in their sample. Thus, in spite of the general pattern of long-term monogamy, philopatry, and relatively short natal dispersal distances, new pair bonds may be formed during the winter, leading to occasional gene flow among populations.

Swainson's Hawks are related to a nonmigratory island endemic species, Galapagos Hawk (*B. galapa-*

goensis), which has a very high within-island genetic uniformity, indicative of small founder populations and high levels of inbreeding (Bollmer et al. 2005). The genetics of the Illinois population of Swainson's Hawk parallels that of Galapagos Hawk in that genetic variation probably was lost due to small population size and subsequent inbreeding. On the other hand, the high level of between-population band-sharing suggests fairly recent isolation or mixing during the nonbreeding season. If the Illinois population is a remnant of a formerly continuous distribution, its isolation most likely corresponds to the wide-scale conversion of prairie to row-crop agriculture during the mid to late 1800s. Swainson's Hawks can tolerate some agriculture, but in Illinois corn and soybean monocultures dominate the landscape and are much less suitable for the hawks than pastures, hay, and small grains (England et al. 1997).

Although most Swainson's Hawks migrate to South America, it is possible that the Illinois birds migrate to Florida instead. Swainson's Hawks are considered rare but regular in winter in south Florida (England et al. 1997). Locating the nonbreeding range of the Illinois population will help determine the extent to which the Illinois birds constitute a distinct population from the western birds.

Our results may have been biased because of small sample size, but that was unavoidable given the small population size in Illinois. A more detailed genetic study using DNA minisatellite markers is needed to clarify the patterns we found in this study. Genetic work on additional populations of Swainson's Hawks would help put in perspective the low genetic variability in Illinois with patterns of genetic diversity across the geographic range.

The number of Swainson's Hawk nests we found in 2003 is within the range of those reported annually in this area over the past 30 yr. However, like other researchers (Morgan and Morgan 2005), we concentrated our efforts in areas that had nests recently and we may have missed nests farther away. An extensive volunteer effort undertaken in 2006 found five nesting pairs and several observations of single birds of unknown breeding status (V. Berardi and R. Morgan unpublished data). Thus, we believe our estimate of five breeding pairs and a population of up to 16 adults is close to the total population in this area.

The fate of the Illinois Swainson's Hawk population will likely be determined in the next decade. Although the apparent stability of the population during the last 30 yr is cause for optimism, the area where Swainson's Hawks occur is one of the most rapidly developing areas of the state (CRBC 1999). In particular, pastures, hay fields, and other potentially suitable habitat are being converted to subdivisions, strip malls, highways, and other unsuitable habitats. These changes likely reduce food supply and nesting areas, and increase disturbance at nests. If so, the low reproductive success will likely continue and may not be sufficient to maintain the population. Protecting the few nest sites should be relatively easy, but the survival of the Swainson's Hawk population in Illinois will depend on the preservation of adequate foraging habitat and on an understanding of the genetic challenges facing this isolated population.

Acknowledgments

We gratefully acknowledge funding from the Illinois Endangered Species Protection Board and the National Science Foundation. Thanks to Liane Cordle and Tari Tweddale for preparing Figure 1. Thanks to Larry O'Neal, Bob Morgan, and Bob Montgomery for help finding nests. We also thank William G. Mattox and James O. McKinley of the Conservation Research Foundation, Boise, Idaho, and Julie Mulholland of Idaho Fish and Game for collecting and preparing the blood samples from Idaho. Comments from R. Nÿboer, W. Gibbons, C.S. Houston, an anonymous reviewer, M.I. Goldstein, and C. Dykstra greatly improved the manuscript.

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Received 7 March 2006; accepted 12 August 2006
Associate Editor: Michael I. Goldstein