The Condor 113(4):768–778

NEST-SITE FIDELITY AND DISPERSAL OF GYRFALCONS ESTIMATED BY NONINVASIVE GENETIC SAMPLING

Travis L. Booms[1,5], Sandra L. Talbot[2], George K. Sage[2], Brian J. McCaffery[3], Kevin G. McCracken[1], and Philip F. Schempf[4]

[1]*Biology and Wildlife Department and Institute of Arctic Biology, University of Alaska, 211 Irving I, Fairbanks, AK 99775*
[2]*U.S. Geological Survey, Alaska Science Center, 4210 University Dr., Anchorage, AK 99508*
[3]*U.S. Fish and Wildlife Service, Yukon Delta National Wildlife Refuge, P.O. Box 346, Bethel, AK 99559*
[4]*U.S. Fish and Wildlife Service, Migratory Bird Management—Raptors, 3000 Vintage Blvd., Suite 240, Juneau, AK 99801*

Abstract. We used feathers from adult Gyrfalcons (*Falco rusticolus*) molted in breeding territories and blood samples from nestlings to document nest-site fidelity and dispersal of breeding adults and juveniles at three areas 100–350 km apart in Yukon Delta National Wildlife Refuge, Alaska, 2003–2007. We used genotypes from seven polymorphic microsatellite loci that provided a mean probability of identity of 0.91×10^{-5}. Breeding Gyrfalcons were highly faithful to study area and territory; we documented no dispersals of breeding birds among study areas and only one dispersal between territories. But their fidelity to nest sites was low; 22% of birds returned to the same nest site the following year. Distance among alternate nests within a territory averaged 750 m and was similar for both sexes. Mean tenure in a territory was 2.8 years, similar for both sexes, and distributed bimodally with peaks at 1 and 4 years. Mean annual turnover rate at the Ingakslugwat Hills (Volcanoes) study area was 20%. We detected three young that established breeding territories at distances ranging from 0 to 254 km from their natal territory, representing 2.5% apparent recruitment. Gyrfalcons in the Askinuk Mountains study area were slightly but statistically significantly differentiated genetically from those in the Volcanoes and Kilbuck Mountain study areas. These data are the first published on the nest-site fidelity, breeding dispersal, and natal dispersal of the Gyrfalcon in North America and demonstrate the utility of noninvasive genetic sampling to greatly improve our understanding of avian dispersal and its underlying mechanisms.

Key words: *Alaska, Arctic,* Falco rusticolus*, falcon, genetic tagging, movements, raptor.*

Fidelidad al Sitio de Anidación y Dispersión de *Falco rusticolus* Estimados Mediante Muestreos Genéticos No Invasivos

Resumen. Utilizamos plumas de individuos adultos de la especie *Falco rusticolus* que habían sido mudadas en territorios de cría y muestras de sangre de pichones para documentar la fidelidad a los sitios de anidación y la dispersión de adultos reproductores y aves jóvenes en tres áreas separadas por 100–350 km en el Yukon Delta National Wildlife Refuge, Alaska, entre 2003 y 2007. Empleamos los genotipos de siete loci microsatélites polimórficos, que brindaron una probabilidad media de identidad de 0.91×10^{-5}. Los individuos reproductores fueron altamente fieles a las áreas de estudio y a sus territorios. No documentamos movimientos entre áreas de estudio y sólo registramos un evento de dispersión entre territorios. Sin embargo, la fidelidad a los sitios de anidación fue baja. El 22% de las aves regresó al mismo sitio de anidación al año siguiente. La distancia promedio entre nidos alternos dentro de un territorio fue de 750 m y fue similar para ambos sexos. El tiempo medio de permanencia en un territorio fue de 2.8 años, fue similar entre sexos y se distribuyó bimodalmente, con picos en 1 y 4 años. La tasa media de recambio anual en el área de estudio de las colinas Ingakslugwat (volcanes) fue 20%. Detectamos tres aves jóvenes que establecieron territorios a distancias de 0 a 254 km de su territorio natal, lo que representa un reclutamiento aparente del 2.5%. Los individuos del área de estudio de las montañas Askinuk eran ligeramente pero significativamente diferentes genéticamente de aquellos de las áreas de estudio de los volcanes y de la montaña Kilbuck. Estos son los primeros datos publicados sobre la fidelidad a los sitios de anidación y sobre la dispersión de *F. rusticolus* en América del Norte. Además, demuestran la utilidad de los muestreos genéticos no invasivos para aumentar de forma considerable nuestro conocimiento sobre la dispersión de las aves y sus mecanismos subyacentes.

INTRODUCTION

Dispersal is one of the most important life-history traits determining a species' persistence and evolution (Hanski 1999, Wiens 2001) and includes both breeding dispersal (movement between breeding locations) and natal dispersal (movement from natal origin to location of first breeding) (Greenwood and Harvey 1982). Documenting dispersal behaviors and patterns

Manuscript received 13 September 2010; accepted 11 May 2011.
[5]Current address: Wildlife Diversity Program, Alaska Department of Fish and Game, 1300 College Rd., Fairbanks, AK 99701.
E-mail: travis.booms@alaska.gov

The Condor, Vol. 113, Number 4, pages 768–778. ISSN 0010-5422, electronic ISSN 1938-5422. DOI: 10.1525/cond.2011.100178

allows for a greater understanding of population dynamics, metapopulation structure, and conservation status, particularly for rare or isolated populations (Fahrig and Merriam 1994, Pearce and Talbot 2006, Davis and Shaw 2001). However, dispersal is difficult to study, especially in long-lived species capable of dispersing long distances (Turchin 1998).

Recent applications of non-invasive genetic mark–recapture sampling allow researchers to investigate aspects of a species' life history and ecology that were previously not accessible (Taberlet and Luikart 1999, Bayard DeVolo et al. 2005, Waits and Paetkau 2005, Alcaide et al. 2010). Though non-invasive genetic sampling is common in mammalogy (Waits and Paetkau 2005, Prugh et al. 2005, Robinson et al. 2009), its use in ornithology is still rare (Morrison and Wood 2009), and suitable markers and methods are unavailable or just being developed for many species (Alcaide et al. 2010). Though the technique has been used to investigate the biology and population status of a few species of raptors (Rudnick et al. 2005, 2008, Bayard DeVolo 2005, Alcaide et al. 2010), its use to study dispersal and nest-site fidelity in raptors has been lacking. Non-invasive genetic sampling can thus provide a better understanding of dispersal because it may allow researchers to follow many individuals across time and space much more readily and easily than do traditional mark–recapture methods.

Most raptors are believed to have high fidelity to a breeding territory (e.g., Jenkins and Jackman 1993, Rosenfield and Bielefeldt 1996, Steenhof et al. 2005). Raptors return to familiar sites because familiarity with a habitat and a mate can increase breeding success (Newton 1979, Bradley et al. 1990, Reese et al. 1996). However, dispersal can also be beneficial by allowing individuals to respond to variable habitat, population density, and potential inbreeding (Clobert 2001). Dispersal behaviors in raptors and their underlying mechanisms are largely unknown because of the difficulties inherent in tracking highly mobile, often secretive species across large landscapes (Linkhart and Reynolds 2007). For example, we lack substantial information on dispersal of some of the most abundant raptors in North America, including the Sharp-shinned Hawk (*Accipiter striatus*) (Bildstein and Meyer 2000) and Broad-winged Hawk (*Buteo platypterus*) (Goodrich et al. 1996).

The Gyrfalcon (*Falco rusticolus*) is the largest falcon, and, because it breeds at low densities in remote, arctic regions of the circumpolar north, its dispersal and fidelity behaviors are generally unknown. The current population estimate for Alaska is 375–635 breeding pairs (Swem et al. 1994, Booms et al. 2009), and the world population is thought to be 8000–11 000 pairs. Gyrfalcons have large home ranges and can undertake long-distance, intra- and inter-continental movements of >1000 km (Burnham 2007, McIntyre et al. 2009). They are known to live at least 12 years in the wild (Cade et al. 1998) and are thought to first breed in their third year of life (Booms et al. 2008a). Some historical nest sites have been used repeatedly for centuries (Burnham 2007), but individuals' fidelity to nest sites and territories and their patterns of use of alternate nests are generally unknown. Anecdotal observations of uncommon color variants and fidelity of two marked females in Iceland (Nielsen 1991) suggest that some individuals remain faithful to breeding territories. However, no other published data are available and, to our knowledge, none exist in the literature on dispersal or site fidelity of marked birds anywhere outside of Iceland.

Therefore, we used non-invasive genetic sampling to investigate Gyrfalcon dispersal and fidelity for the first time in North America. From 2003 to 2007, we assessed movements of individual birds by recapturing their genotypes in molted feathers collected from three study areas in Yukon Delta National Wildlife Refuge (Yukon Delta NWR) in western Alaska. Our objective was to record novel quantitative data describing the Gyrfalcon's nest-site fidelity, breeding dispersal, and natal dispersal and to use these findings to highlight the utility of non-invasive genetic sampling for studying the birds' movements at large spatial and temporal scales.

METHODS

STUDY AREA

For genetic analysis, we collected molted feathers from Gyrfalcons in three areas of Yukon Delta NWR: Ingakslugwat Hills (hereafter called the Volcanoes), Askinuk Mountains, and Kilbuck Mountains (Fig. 1). We selected study sites nonrandomly on the basis of the presence of relatively large numbers of breeding Gyrfalcons in accessible locales. The Volcanoes (61° 21′ N, 164° W) were our primary study area, covering approximately 600 km^2. It is dominated by small, inactive volcano craters less than 1 km wide and rising up to 200 m in elevation. The study area is surrounded by the vast lowland deltas of the Yukon and Kuskokwim rivers, and almost no cliffs are available as nesting habitat for approximately 70 km in any direction. The volcanoes, associated lava flows, and several isolated stands of balsam poplars (*Populus balsamifera*) serve as the area's only substrate for Gyrfalcon nests. The study area contains among the highest concentrations of nesting Gyrfalcons ever documented with a mean distance between nests of 3.9 ± 2.2 km (BJM, unpubl. data). Typically, seven to nine Gyrfalcon territories are occupied annually, and most of these successfully produce young (TLB, unpubl. data). We collected molted feathers from this study area from 2003 ot 2007 and blood samples from nestlings from 2004 to 2007 (Table 1).

The Askinuk Mountains study area (61° 45′ N, 164° 45′ W) is located 100 km northwest of the Volcanoes across the lowland delta of the Yukon River. It is a small mountain range on the coast of the Bering Sea with a maximum elevation of 700 m (Fig. 1). Surrounding the study area on three

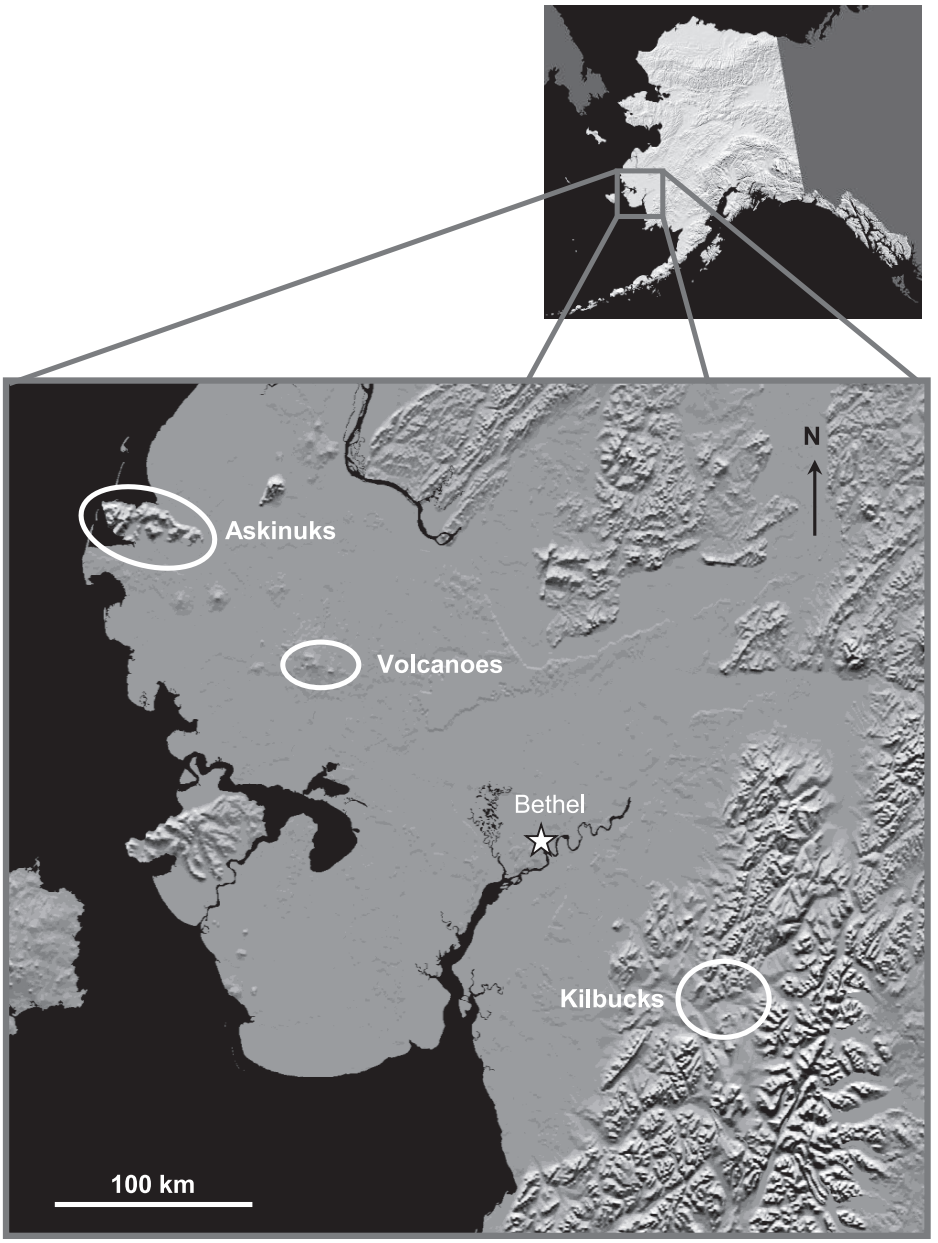

FIGURE 1. Study areas on the Yukon Delta National Wildlife Refuge from which Gyrfalcon genetic samples were collected, 2003–2007.

sides are highly productive wetlands that support large numbers of breeding waterfowl and shorebirds. The area includes approximately 1000 km^2 of rolling upland tundra. Gyrfalcons and other raptors nest on the numerous isolated tors reaching up to 80 m in height that are scattered throughout the study area. Like the Volcanoes study area, the Askinuks are essentially an island of breeding habitat surrounded by wetland tundra or water and typically support eight to ten occupied Gyrfalcon territories annually. Though potential nest cliffs in the Askinuks are more numerous than in the Volcanoes, the cliffs are more dispersed, and the mean distance between nests is higher (6.1 ± 4.1 km; BJM, unpubl. data). We collected molted feathers and blood samples from nestlings from this study area in 2006 and 2007 (Table 1).

The Kilbuck Mountains study area (60° 21′ N, 160° W) is approximately 250 km southeast of the Volcanoes and 350 km from the Askinuks. The area is separated from the Volcanoes and Askinuks by a vast expanse of wetland tundra and boreal forest with essentially no cliffs for nesting in between (Fig. 1). The study area covers approximately 2000 km^2 and includes much of the Kisaralik and Kwethluk River watersheds. The area consists of large, open valleys and low mountains reaching up to 975 m in elevation. The Kilbucks study area is surrounded by large tracts of habitat with cliffs that support

TABLE 1. Number of adult Gyrfalcon feathers collected per territory per year in Yukon Delta National Wildlife Refuge, Alaska, 2003–2007.

Study area	2003	2004	2005	2006	2007	Totals[a]
Volcanoes						
Number of known occupied territories	7	9	8	8	9	10
Number of territories from which feathers were collected	6	8	8	8	9	10
Total number of feathers collected	31	69	223	220	437	980
Mean number of feathers collected per territory	5	9	28	28	49	24
Minimum and maximum number of feathers collected per territory	0, 14	0, 19	16, 45	11, 37	17, 92	0, 92
Askinuks						
Number of known occupied territories	—	—	—	9	8	9
Number of territories from which feathers were collected				9	8	9
Total number of feathers collected				188	135	323
Mean number of feathers collected per territory				21	17	19
Minimum and maximum number of feathers collected per territory				6, 44	1, 38	1, 44
Kilbucks						
Number of known occupied territories	—	—	7	5	—	11
Number of territories from which feathers were collected			7	4		10
Total number of feathers collected			27	17		44
Mean number of feathers collected per territory			4	4		4
Minimum and maximum number of feathers collected per territory			1, 7	0, 7		0, 7

[a]For number of known occupied territories and territories from which feathers were collected, totals are the number of unique territories sampled across years.

additional breeding Gyrfalcons. The mean distance between nests is 6.3 ± 4.7 (BJM, unpubl. data), and the area typically supports 8–11 occupied Gyrfalcon territories annually. The cliffs are generally larger, more numerous, and more complex than those in the other study areas, and we found relatively few feathers at territories because of this. We colleced molted feathers and blood samples from nestlings in the Kilbucks in 2005 and 2006.

DEFINITIONS OF TERMINOLOGY

We define *nest site* as a ledge or stick nest, whether on a cliff or in a tree, that contained Gyrfalcon eggs or young at any point in the present or past. *Dispersal* is the movement between consecutive nest sites or between a natal nest site and place of first breeding; *dispersal distance* is the straight-line distance between these two nest sites as measured in GIS. *Territory* is an area surrounding an occupied nest site in which no other Gyrfalcons were observed nesting concurrently during our study or previous surveys (Newton and Marquiss 1982). Nest sites within a territory used by resident birds are considered alternate nests. The same territories were typically occupied and sampled during each year of the study. Hence, data reflect the total number of instances that territories were occupied and not the total number of unique territories sampled. *Occupied* refers to a territory with one or more adults observed or detected, regardless of breeding status. *Active* nest sites contained eggs or young. A *unique individual* is a bird represented by a consensus genotype that we obtained independently from five or more feather samples or, if obtained from two to four samples, differed from other genotypes by at least two alleles and that we considered a resident. A *resident bird* is a unique individual detected at a territory and met at least one of the following conditions: (A) it was the only individual of that sex detected at a territory that year, (B) it was a parental match to the genotype of nestlings present, (C) if no nestlings were sampled, it had the most frequent genotype of an adult of that sex detected in feathers at that site that year, or (D) it was defending young and reading of its color band confirmed its identity. An *occasion* is the detection of a unique individual at one territory in one year, regardless of the number of samples in which it was detected that year. *Old feathers* are those that were molted during the previous breeding season, overwintered in the study area, and were distinguishable from fresh feathers by the presence of mold, algae, or well-separated barbs (Booms et al. 2008b). *Fresh feathers* are those that were molted during the current breeding season and identified as such by the criteria of Booms et al. (2008b). *Annual turnover* is the number of occasions on which an adult was known to be replaced on a territory divided by the total number of occasions on which the identity of an adult at a territory was known in consecutive years (Linkhart and Reynolds 2007). *Territory tenure* is the total number of consecutive

years that a unique individual occupied the same territory during our 5-year study (Linkhart and Reynolds 2007). *Apparent recruitment* is the number of breeding birds that were initially sampled as nestlings in our study areas divided by the total number of nestlings from which we collected blood samples.

SAMPLE COLLECTION

Gyrfalcons breeding south of 70° N are thought to be nonmigratory (though see Burnham 2007) and, on the basis of movements of two adult females harnessed with satellite transmitters in the Volcanoes study area, adult Gyrfalcons in Yukon Delta NWR likely reside on their territories year round (PFS, unpubl. data). In Alaska, Gyrfalcons begin molting feathers in early or mid-April during courtship, continue molting more or less continually throughout the breeding season, and complete molt in mid-late September, with differences by sex and feather tract (Booms et al. 2008a). Hence, molted feathers from breeding pairs can be commonly found near Gyrfalcon nests from April through the breeding season.

We attempted to collect molted adult Gyrfalcon feathers from perches, nests, and below nests at all occupied Gyrfalcon territories in our study areas annually. The timing of collection varied by year and study area. In 2003, we visited territories in the Volcanoes after young had fledged. From 2004 to 2006, we collected feathers at territories in the Volcanoes multiple times opportunistically from pre-incubation (April) to post-fledging (July). In 2007, we collected feathers at the Volcanoes multiple times opportunistically during incubation (May) and the nestling phase (June). We visited sites in the Askinuks and Kilbucks only once in late June to collect molted feathers and blood samples from nestlings. In all study areas following common avian blood-sampling protocols (Monk and Forbes 2007), we collected blood quills or blood from the brachial vein of nestlings. In the field, blood was stored in preservation buffer (Longmire et al. 1988) at ambient temperature, then frozen at –80 °C until DNA was extracted. We placed feathers in individual paper envelopes stored in Ziploc bags containing silica desiccant until DNA was extracted. Because Rough-legged Hawks (*Buteo lagopus*), Golden Eagles (*Aquila chrysaetos*), and Peregrine Falcons (*Falco peregrinus*) occurred in the study areas, we identified molted feathers to species in the field visually by size and plumage patterns. All non-Gyrfalcon samples were separated and archived.

We captured five adult breeding Gyrfalcons in the Volcanoes, banded each with a uniquely coded color band, and drew blood from each for genetic identification. Subsequent resighting of two of these individuals and collection of their feathers over 4 years of the study provided independent tests of genetic identification. We treated data from males and females independently throughout. Because most nests were not visited after late June, their fate was unknown in most instances.

We extracted whole genomic DNA from blood and bloodquill samples by protocols described in Medrano et al. (1990) and modified by substitution of 0.7 volumes of 2-propanol in place of two volumes of ethanol. DNA was extracted from feathers by the same protocol, with the following exceptions: (1) dithiotrhreitol (0.1 mg mL^{-1}) was added to the lysis buffer, (2) 1% glycogen was added to the DNA-precipitation step, and (3) lysis proceeded for up to 5 days. We quantifed the extracted genomic DNA by fluorometry and diluted the extractions to working solutions of 50 ng μL^{-1}.

MICROSATELLITE DNA GENOTYPING AND MOLECULAR SEXING

We genotyped samples at each of seven autosomal microsatellite loci with primers developed specifically for the Peregrine Falcon and known to be polymorphic in the Gyrfalcon: NVHfp, 13-1, 34, 54, 79-4, 82-2, 89-2, 92-1 (Nesje et al. 2000, Nesje and Røed 2000). For genotyping, we used the universal tailed primer approach (Oetting et al. 1995) as described for microsatellite loci in Sonsthagen et al. (2004). We carried out amplifications in a final volume of 10 µL that contained 1 µL DNA extract, 0.2 mM dNTPs, 0.1 µg μL^{-1} bovine serum albumin (BSA), 1× PCR buffer (Perkin Elmer Cetus I; PE Biosystems, Forest City, CA), 10.0 pmoles unlabeled primers, 1.0 pmoles fluorescently labeled universal primer, and 0.3 units Taq polymerase (U.S. Biochemical, Cleveland, OH). The PCR began at 94 °C for 90 sec and continued with 40 cycles each of 94 °C for 30 sec, 50–56 °C for 30 sec, and 72 °C for 60 sec. We concluded each reaction with a final extension at 72 °C for 30 min. We electrophoresed PCR products on a 48-well 25-cm 6% polyacrylamide gel on a LI-COR 4200LR automated sequencer (LI-COR, Inc., Lincoln, NE). We designated allele sizes by referencing an M13 DNA sequence ladder. We used samples of scored individuals on subsequent gels to size new genotypes with Gene ImagIRe 4.05 software (Scanalytics, Inc., Fairfax, VA). For quality control, we extracted, amplified, and genotyped 10% of the samples in duplicate.

We sexed each bird by PCR amplification of the CHD gene, using protocols similar to those outlined in Handel et al. (2006) and the P8/P2 primer set (Griffiths et al. 1998). We performed PCR on a RoboCycler Gradient 96 (Stratagene Corporation, La Jolla, CA). We carried out PCR amplifications of DNA in a final volume of 10 µL containing 1 µL of DNA extract, 1× PCR buffer (Perkin Elmer Cetus I), 0.2 mM deoxyribonucleotide triphosphate (dNTP), 3.6 pmoles unlabeled forward P8 primer, 4.0 pmoles unlabeled reverse P2 primer, 0.4 pmoles labeled P8 primer, 0.1 µg μL^{-1} BSA, and 0.75 units Taq polymerase (U.S. Biochemical). The PCR began at 94 °C for 90 sec, continued with 40 cycles each of 48 °C for 45 sec, 72 °C for 45 sec, and 94 °C for 30 sec, and concluded with a final annealing and extension step of 48 °C for 60 sec and

72 °C for 5 min. We electrophoresed PCR products on a 48-well 18-cm 6% polyacrylamide gel on a LI-COR 4200LR automated sequencer.

In Gyrfalcons, the reaction yielded a 403-base-pair (bp) product from the Z-chromosome (both males and females) and a 424-bp product from the W-chromosome (females only). We assigned sex on the basis of the absence (male: ZZ) or presence (female: ZW) of the W-chromosome PCR product. Because allelic dropout can cause relatively high error rates in the sexing of samples (Gebhardt and Waits 2008), we assigned sex only after obtaining consensus genotypes from multiple independent feathers (see Data Processing below).

DATA PROCESSING

Feathers contain only small amounts of DNA and are prone to errors of genotyping including allelic dropout, false alleles, and scoring errors (Waits and Paetkau 2005, Hogan et al. 2007). Such errors can affect classification of an individual significantly and cause an excess of genotypes to be observed (Lukacs and Burnham 2005). To avoid including erroneous genotypes in analyses, we followed a conservative approach, strict laboratory procedures with liberal culling of samples, and published guidelines as suggested by Waits and Paetkau (2005). Because we were not interested in estimating the number of individuals present in samples, we took an even more conservative approach by using only genotypes that were found in multiple independent samples. Using independently replicated consensus genotypes increases the probability of accurate genotypes (Waits and Paetkau 2005). Therefore, we accepted all genotypes detected in five independent samples as correct. We accepted genotypes replicated in two to four samples ($n = 11$) only if they differed from all other genotypes by two or more alleles. Because genotyping errors should be random, the probability of observing the same errors at multiple loci in multiple samples is low (Waits and Leberg 2000). Hence, our dataset is a conservative representation of the number of birds present in our samples, but this conservatism provided us high confidence in the accuracy of our individual identifications used to assess dispersal and fidelity.

GENETIC DIVERSITY

We calculated levels of genetic diversity and probability of identity from a sample of nestlings (one nestling per nest) pooled from the three study areas. Mean number of alleles (A) and observed and expected heterozygosities (H_O and H_E) were calculated in Genepop version 3.3 (Raymond and Rousset 1995). We tested each microsatellite locus in the putative populations (Askinuks, Volcanoes, and Kilbucks) for deviation from Hardy–Weinberg equilibrium, with the Markov-chain parameters provided (dememorization number = 10 000, number of batches = 100, and number of iterations per batch = 5000). Since loci were not mapped to chromosomes, we tested each pair of loci within each population for linkage disequilibrium in Genepop with the Markov-chain parameters provided. We used Queller and Goodnight's (1989) relatedness (*rxy*), as implemented in the program Identix (Belkhir et al. 2002), to determine the average level of relatedness among eight pairs of resident birds within the Askinuks and the Volcanoes.

INDIVIDUAL IDENTIFICATION

We identified matching seven-locus genotypes from those obtained from all molted feathers with Microsatellite Toolkit (Park 2001). After testing the loci for linkage disequilibrium and Hardy–Weinberg equilibrium, we used the software Gimlet version 1.3.2 (Valière 2002) to calculate $P_{(ID),}$ the probability that another individual with the same genotype would be observed given the sample frequency of the alleles observed at those loci within the target population. Unrelated nestlings (one per nest, $n = 23$) from all populations were pooled for these analyses. General guidelines (e.g., Taberlet and Luikart 1999) for identifying individuals by microsatellite loci suggest using a suite of markers that achieves a reasonably low $P_{(ID)}$ bounded between 0.01 and 0.0001.

POPULATION DIFFERENTIATION

We assessed spatial variation in allelic frequency among the Askinuks, Volcanoes, and Kilbucks with F- and R-statistics, which describe the apportionment of allelic variance among individuals within and among populations, respectively (Wright 1951, Weir and Cockerham 1984, Slatkin 1995). Though we had no a priori knowledge of whether birds in these study areas constituted distinct populations, we used these designations to define putative populations for analyses. We obtained multilocus estimates of F_{ST} and R_{ST} with FSTAT and Arlequin (Excoffier et al. 2005), using 18, 25, and 8 unique individuals to represent the Askinuks, Volcanoes, and Kilbucks study areas, respectively. These individuals were paired adults, or, in cases where adults were not sampled, were one nestling per territory (that is, we avoided including known first-order relatives in the analyses). We used Hedrick's (1999, 2005) method to calculate the maximum value of F_{ST} obtainable from the microsatellite loci and assessed significance in Arlequin with 10 000 random permutation tests, in which alleles of two populations were permuted randomly. We used Bonferroni correction factors to evaluate significance for multiple comparisons.

Because R_{ST} assumes a stepwise model of microsatellite mutation, R-statistics are considered more appropriate than F-statistics, which assume an infinite-alleles model (Slatkin 1995). However, for populations that have diverged very recently or are still connected via continuing gene flow, F-statistics generally provide estimates of differentiation better than do R-statistics because migration and drift are relatively more important forces acting on the populations than is mutation (Slatkin 1995).

STATISTICAL ANALYSIS

We used Mann–Whitney U-tests executed in Statistics Online Computational Resource (Dinov 2006) to determine if males and females were detected in equal numbers in feather

samples, if dispersal distance differed by study area, and if pairwise relatedness of resident birds differed by study area. We collected relatively few feathers from nest sites in the Kilbucks, and we detected no adults in multiple years there. Hence we do not include data from this area in analyses unless stated. We used only data from the Volcanoes to assess tenure and turnover because other areas were sampled in only 2 years. We report all results as mean ± SD and consider results significant at $P = 0.05$.

RESULTS

FEATHER AND BLOOD SAMPLES

We collected 1347 molted feathers from adults in occupied territories at the three study areas over the 5 years (Table 1). From these, across all years, we detected 43 unique individuals in 570 feathers that we identified as representing resident birds in the Askinuks and Volcanoes study areas. The numbers of males ($n = 19$) and females ($n = 24$) detected were similar. Though we detected additional individuals in feather collections, they failed to meet the definition of a unique individual or a resident bird and excluded them from analyses. The number of feathers in which an individual was detected at a territory each year varied greatly, from zero to 34. Males were detected in fewer feathers per site per year than were females (males 3.7 ± 3.0, $n = 36$; females 8.2 ± 7.2, $n = 52$; $U = 557$, $P < 0.001$). We collected blood samples from 121 nestlings from 44 of 54 known broods across all years and study areas.

GENETIC DIVERSITY AND RELATEDNESS

The suite of seven loci gave us a mean probability of identity (P_{ID}) = 0.91 × 10^{-5} (Table 2). No significant deviations from Hardy–Weinberg equilibrium for the pooled samples were observed for any locus ($P = 0.069$ to 1.000) or overall ($\chi^2 = 9.682$, df = 14.0, $P_{global} = 0.785$). Among a total of 21 comparisons, we detected linkage disequilibrium between three pairs of loci (FP13–FP34; FP13–FP79; FP34–FP92-1), which was higher than expected at random ($P > 0.01$). Subsequent analyses of data by population, rather than pooled, failed to detect a signature of linkage disequilibrium, suggesting that the observed disequilibrium was due to admixture of samples from individuals representing more than one discrete population (see below).

Mean r_{xy} pairwise relatedness from 16 pairs of resident birds was –0.023 ± 0.39. Pairwise relatedness of resident pairs in the Askinuks (–0.066 ± 0.42, $n = 8$) and Volcanoes (–0.044 ± 0.37, $n = 8$; $U = 32$, $P > 0.5$) was not significantly different.

FIDELITY AND POPULATION DIFFERENTIATION

Of 37 occasions on which we determined the location of consecutive nests, birds returned to the same nest in the following year in only eight instances (22%). Four unique males and three unique females were responsible for these instances at five unique territories. Of the 46 occasions for which we could ascertain fidelity to a territory in consecutive years, birds returned to the same territory on 45 occasions (98% territory fidelity). In the Volcanoes, mean territory tenure was 2.8 ± 1.4 years, similar for both sexes (males 2.6 ± 1.3 years, females 2.9 ± 1.6 years), and distributed bimodally with peaks at 1 and 4 years (Fig. 2). Mean annual turnover rate at the Volcanoes was 20%. We detected low but statistically significant differentiation (both F_{ST} and R_{ST}) between birds in the Askinuks study area and those in the other two study areas (Table 3). Differentiation between the Volcanoes and Kilbucks was not significant.

TABLE 2. Summary of the variation in microsatellite loci used to identify individual Gyrfalcons ($n = 43$) in Yukon Delta National Wildlife Refuge, Alaska, 2003–2007.

Locus[a]	Range in allele size (bp)	Number of alleles/ locus	Observed hetero-zygosity	Expected hetero-zygosity	Probability of identity (PID)
FP13	118–124	4	0.36	0.46	0.31
FP34	168–174	4	0.52	0.51	0.37
FP54	109–145	11	0.71	0.82	0.04
FP79-4	171–183	6	0.62	0.60	0.23
FP82-2	157–169	5	0.48	0.55	0.21
FP89-2	141–163	5	0.36	0.35	0.48
Fp92-1	129–139	4	0.19	0.19	0.70
Combined	—	5.6	0.46	0.50	0.91×10^{-5}

[a]No significant deviations from Hardy-Weinberg equilibrium observed for any locus.

BREEDING DISPERSAL

Individuals moved to a new nest on 29 of the 37 occasions (78%), and the proportion of females using new nests (83%) appeared slightly higher than that of males (71%). Dispersal distances based on genotypes recaptured from feathers ranged from 50 to 3400 m, averaged 750 ± 870 m, and were similar in both sexes (females 754 ± 950 m, $n = 19$; males 745 ± 740 m, $n = 10$). The longest distance moved between alternate nest sites was 2300 m. The mean distance moved was 1725 ± 1080 m in the Askinuks ($n = 4$) and 595 ± 745 m in the Volcanoes ($n = 25$), though the difference was not statistically significant ($U = 22.5$, $P = 0.08$). We detected one instance of dispersal between territories; a female in the Volcanoes moved 3400 m to a territory where the resident female had died the previous winter (death confirmed via telemetry). We detected no other cases of dispersal between territories and no breeding dispersal from one study area to another. There were six instances in which we detected an individual the year after it did not appear to breed or its nest failed. In all instances, the bird returned to breed in the same territory the following year.

NATAL DISPERSAL

We detected three instances of natal dispersal representing 2.5% apparent recruitment. One male nestling was detected

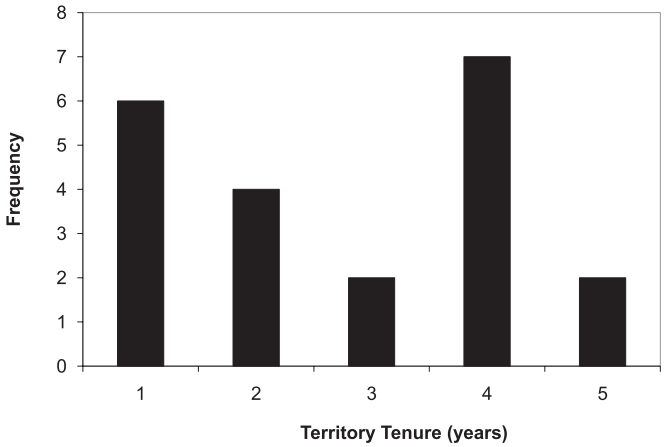

FIGURE 2. Total number of consecutive years for which a unique individual Gyrfalcon was detected at the same territory in the Volcanoes study area in Yukon Delta NWR from 2003 to 2007.

in its third year of life in 11 feathers at a site 11.6 km from its natal site in the Volcanoes. We read its color band, and it was a parental match to the two nestlings in the nest. The bird was not detected in any samples during its second year of life. A female that was sampled and color-banded as a nestling at a different nest in the Volcanoes was detected in four molted feathers at its natal site 2 years after fledging. The bird was a parental match to the three nestlings present. We made no effort to resight bands at that site and did not detect the bird in the interim year. The mother of the bird was not detected in the study area the year in which she was replaced by her daughter. The third case of natal dispersal was of a female that moved 254 km from its natal site in the Volcanoes to the site of its apparent first breeding in the Kilbucks, where it was detected as a third-year bird in two molted feathers. We made no effort to resight color bands at that site. This female was a parental match to all three nestlings present, and we detected no other female genotype at that site that year. It was not detected during the interim year.

DISCUSSION

These results are the first data published on the Gyrfalcon's nest-site fidelity, breeding dispersal, and natal dispersal in North America or for any continental population of the species. Therefore, this study demonstrates the unique ability of non-invasive genetic sampling of molted feathers to advance our understanding of dispersal and fidelity in raptors and likely other birds difficult to study.

At our study sites, Gyrfalcons were highly faithful to study areas and territories but regularly moved short distances among alternate nest sites. Three instances of natal dispersal demonstrated that Gyrfalcons undertook both long- and short-distance movements from their natal areas to their first breeding site. Within the 5-year study period, we saw a bimodal distribution of territory tenure, possibly suggesting most birds' tenure at territories is either short (1 year) or long (≥4 years). From the low but significant genetic structure, it appears dispersal between the Askinuks and other study areas was limited, whereas a lack of significant structure suggests higher levels of gene flow between the Volcanoes and Kilbucks, as was corroborated by an instance of natal dispersal between these study areas.

FIDELITY AND POPULATION DIFFERENTIATION

In our study areas, Gyrfalcons were philopatric to the study area in which they were first detected breeding. We observed no breeding dispersals among study areas and found low but statistically significant differentiation between the Askinuks and the other two study areas. We detected no significant differentiation between the Volcanoes and Kilbucks, and we speculate that gene flow between these areas was facilitated by natal dispersal, as we documented and has been found in other raptors (Wiens et al. 2006). We caution, however, that in spite of the differentiation between Kilbucks and the Askinuks, the low sample size for the Kilbucks may have resulted in a type II error in the comparison between that region and the Volcanoes. Additional sampling of the Kilbucks region would clarify this. Though information on the Gyrfalcon's population differentiation elsewhere is limited, Johnson et al. (2007) used microsatellite markers and found similar but nonsignificant F_{ST} values between two breeding populations in Greenland separated by 1300 km of land, ocean, and glacier. They also found no significant structure between samples taken from Canada and Alaska and between samples taken from Norway and Canada. Possibly, the structure we observed in our study areas could be a result of what appears to be a highly philopatric, nonmigratory population at a lower latitude, whereas the breeding populations sampled by Johnson et al. (2007) were from higher latitudes where Gyrfalcons are thought to be (and in Greenland, have been documented to be) more migratory. Additional analyses and genetic markers are needed for genetic differentiation among our study areas to be understood more fully.

We assumed Gyrfalcons to be faithful to territories, but the only previously available data to support this assumption were from two females banded in Iceland (Nielsen 1991). Data from 24 individuals in our study area over 5 years corroborate this assumption. The only bird that we detected dispersing out of a territory was a female that had been captured and harnessed with a transmitter 2 years prior to the dispersal. The bird escaped from the harness and successfully bred at the same site the year after capture and before dispersing the following year. Hence we think it is unlikely that the bird's movements were influenced by its being harnessed 2 years prior to its dispersal.

North American falcons demonstrate a generally increasing trend of territory fidelity with body size, and our data on the largest species corroborate this trend. The territory fidelity of the smallest species, the American Kestrel (*F. sparverius*) and Merlin (*F. columbarius*), are moderate, 20–70%) (Hodson 1976, Bowman et al. 1987, Toland and Elder 1987, James et al.

1989). Though little information is available for the intermediate sized Aplomado Falcon (*F. femoralis*), fidelity of the Prairie Falcon (*F. mexicanus*) is generally higher, though variable from 43 to 88% (Runde 1987, Lehman et al. 2000). The Peregrine Falcon (*F. peregrinus*), the second-largest North American falcon, is highly site faithful with 93–98% of adults returning to the same territory (Ambrose and Riddle 1988, Enderson and Craig 1988). Gyrfalcons we studied matched the highest known rate of territory fidelity documented in North American falcons (98%, *F. p. tundrius*; Court 1986). Whether or not this trend also applies to other North American raptor genera or how it may be influenced by migratory status is not clear, partially because of a lack of sufficient data on fidelity and dispersal of a majority of species within other genera. Applying non-invasive genetic sampling to other species should allow this question to be addressed more thoroughly in the future.

BREEDING DISPERSAL

The Gyrfalcons we studied were highly faithful to territories but frequently rotated among alternate nest sites within a territory, a common behavior in many raptors (Newton 1979). Similar territory tenacity and use of alternate nest sites has been documented in other North American raptors including accipters (Wiens et al. 2006, Rosenfield and Bielefeldt 1996), buteos (Preston and Beane 2009, Dykstra et al. 2008), and eagles (Jenkins and Jackman 1993). The prevalence of this behavior across raptor genera supports the conclusion that site fidelity likely provides significant fitness benefits to individuals. Like other North American falcons (Warkentin et al. 1991, Lehman et al. 2000), Gyrfalcons moved to alternate nests within a territory after both successful and failed breeding and provided no strong evidence to suggest movements were influenced by nest fate.

NATAL DISPERSAL

Natal dispersal is one of the most important yet poorly known aspects of life history and ecology (Penteriani and Delgado 2009). Though relatively little can be inferred from the first three documented instances of natal dispersal by Gyrfalcons in North America, these data allow some insight into this process. For example, none of the three dispersers was detected in molted feathers until 2 years after it fledged, suggesting natal dispersal and its underlying mechanisms may be a 2-year process. The only other information on natal dispersal in the Gyrfalcon comes from two males and two females that were resighted at nests in Iceland from 14 to 84 km from their natal site (Nielsen 1991), a range that contrasts with the widely variable distances we observed (0, 11, and 254 km).

GENERAL

We selected our study areas nonrandomly because they contained high concentrations of Gyrfalcon nests and were accessible to researchers. Therefore, our estimates should not be interpreted as representative of other areas. Furthermore, because fidelity and dispersal have not been estimated elsewhere, we do not know if our estimates differ from those that would be obtained from areas with lower concentrations of nests.

Two components of detection probability may have biased our estimates. First, individuals that moved beyond our study areas were not available to be detected, and such movements can bias dispersal estimates (Koenig et al. 1996). The range of our estimates is likely biased low because adult and juvenile Gyrfalcons are known to undertake long-distance, sometimes intercontinental movements that far exceed the boundaries of our study areas (Burnham 2007, McIntyre et al. 2009). Similarly, our estimate of recruitment should be considered a minimum because natal dispersals beyond our study areas also could not be detected. Second, even if an individual was available to be detected in our study areas, we may have failed to detect it. This may not have affected our estimates of short-distance breeding dispersal because we searched nearly all available habitat within each study area in the same spatial and temporal manner annually. Hence, missing an occupied site was probably not related to a bird's distance from its previous site within our small study areas. However, failing to detect an individual that was present may have inflated our estimates of fidelity because birds that dispersed to new nests were probably less likely to be detected than birds that returned to previously used nests.

We demonstrated the feasibility of documenting detailed movements of individual birds across hundreds of kilometers of remote, rugged landscapes over a 5-year period by collecting and genotyping molted feathers. Our estimates are the first published on the Gyrfalcon's nest-site fidelity and breeding and natal dispersal in any continental Gyrfalcon population. These data provide a better understanding of the Gyrfalcon's biology, population dynamics, and demography and are the first step toward understanding variables that influence these movements. Our findings add to those of Rudnick et al. (2005, 2008) and Alcaide et al. (2010) in highlighting the usefulness of non-invasive genetic sampling of molted feathers for a detailed understanding of bird movements and fidelity and that the technique may lead to improved understanding of these important behaviors and their underlying mechanisms.

ACKNOWLEDGMENTS

This work was funded by the U. S. Fish and Wildlife Service (USFWS) Yukon Delta National Wildlife Refuge, USFWS Office of Migratory Birds Raptor Management Office, U. S. Geological Survey Alaska Science Center, USFWS's Surveillance Program for Highly Pathogenic Avian Influenza, an Angus Gavin Migratory Bird Research Grant, and an David Burnett Dunn Memorial Research Grant. TLB was supported by a National Science Foundation Research Fellowship, a U.S. Environmental Protection Agency (EPA) Science to Achieve Results Graduate Fellowship, a University of Alaska Thesis Completion Fellowship, and the Alaska Department of Fish and Game Wildlife Diversity Program during various portions of this work. The EPA has not officially endorsed this publication and the views expressed in it may not reflect the views of

the EPA. We thank the staff of the Yukon Delta NWR for providing essential support. M. Fuller, T. Swem, F. Broerman, and T. Doolittle provided essential collaboration. R. Blaedow, N. Dodge, B. Massey, J. Spice, M. Swaim, and B. Torrison provided invaluable assistance collecting field samples. J. Gust, C. R. Dial, and S. Sonsthagen provided curatorial, laboratory, and analytical assistance. We thank R. Rosenfield, K. Blejwas, and M. Patten for helpful comments on earlier versions of the manuscript. Although PFS and BJM are employees of the USFWS, the findings and conclusions in this article are those of the authors and do not necessarily represent the views of the USFWS. Mention of trade names or commercial products does not constitute endorsement or recommendation for use.

LITERATURE CITED

Alcaide, M., L. Cadahia, S. A. Lambertucci, and J. J. Negro. 2010. Noninvasive estimation of minimum population sizes and variability of the major histocompatibility complex in the Andean Condor. Condor 112:470–478.

Ambrose, R. E., and K. R. Riddle. 1988. Population dispersal, turnover, and migration of Alaska Peregrines, p. 677–684. *In* T. J. Cade, J. H. Enderson, C. G. Thelander, and C. M. White [eds.], Peregrine Falcon populations; their management and recovery. Peregrine Fund, Boise, ID.

Bayard DeVolo, S., R. T. Reynolds, J. R. Topinka, B. May, and M. F. Antolin. 2005. Population genetics and genotyping for mark–recapture studies of Northern Goshawks (*Accipiter gentilis*) on the Kaibab Plateau, Arizona. Journal of Raptor Research 39:286–295.

Belkhir, K., V. Castric, and F. Bonhomme. 2002. IDENTIX, a software to test for relatedness in a population using permutation methods. Molecular Ecology Notes 2:611–614.

Bildstein, K. L., and K. Meyer. 2000. Sharp-shinned Hawk (*Accipiter striatus*), no 482. *In* A. Poole and F. Gill [eds.], The birds of North America. Birds of North America, Inc., Philadelphia.

Booms, T. L., T. J. Cade, and N. J. Clum [online]. 2008a. Gyrfalcon (*Falco rusticolus*), no. 114. *In* A. Poole [ed.], The birds of North America online. Cornell Lab of Ornithology, Ithaca, NY. <http://bna.birds.cornell.edu/bna/species/114doi:10.2173/bna.114> (1 June 2010).

Booms, T. L., B. J. McCaffery, and P. Schempf. 2008b. Molted feather persistence and aging in a sub-arctic environment. Condor 110:756–762.

Booms, T. L., F. Huettmann, and P. E. Schempf. 2009. Gyrfalcon nest distribution in Alaska based on a predictive model. Polar Biology 33:347–358.

Bowman, R., J. R. Duncan, and D. M. Bird. 1987. Dispersal and inbreeding avoidance in the American Kestrel: are they related?, p. 145–150. *In* D. M. Bird and R. Bowman [eds.], The ancestral kestrel. Raptor Research Report 6.

Bradley, J. S., R. D. Wooller, I. J. Skira, and D. L. Serventy. 1990. The influence of mate retention and divorce upon reproductive success in Short-tailed Shearwaters (*Puffinus tenuirostris*). Journal of Animal Ecology 59:487–496.

Burnham, K. K. 2007. Inter- and intraspecific variation of breeding biology, movements, and genotype in Peregrine Falcon (*Falco peregrinus*) and Gyrfalcon (*F. rusticolus*) populations in Greenland. Ph.D. dissertation, University of Oxford, Oxford, England.

Cade, T. J., P. Koskimies, and Ó. K. Nielsen. 1998. Gyrfalcon, p. 1–25. *In* D. W. Snow and C. M. Perrins [eds.], Birds of western Palearctic update, vol. 2. Oxford University Press, Oxford, England.

Clobert, J. 2001. Introduction, p. xvii–xvi. *In* J. Clobert, E. Danchin, A. Dhondt, and J. Nichols [eds.], Dispersal. Oxford University Press, Oxford, England.

Court, G. S. 1986. Some aspects of the reproductive biology of tundra Peregrine Falcons. M.Ss. thesis, University of Alberta, Edmonton, Alberta.

Davis, M., and R. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. Science 292:673–679.

Dinov, I. D. 2006. SOCR: statistics online computational resource. Journal of Statistical Software 16:1–16.

Dykstra, C. R., J. L. Hays, and S. T. Crocoll [online]. 2008. Red-shouldered Hawk (*Buteo lineatus*), no. 107. *In* A. Poole [ed.], The birds of North America online. Cornell Lab of Ornithology, Ithaca, NY. <http://bna.birds.cornell.edu/bna/species/107doi:10.2173/bna.107> (1 December 2010).

Enderson, J. H., and G. R. Craig. 1988. Population turnover in Colorado Peregrines, p. 685–688. *In* T. J. Cade, J. H. Enderson, C. G. Thelander, and C. M. White [eds.], Peregrine Falcon populations: their management and recovery. Peregrine Fund, Boise, ID.

Excoffier, L., G. Laval, and S. Schneider. 2005. Arlequin version 3.0: an integrated software package for population genetics data analysis. Evolutionary Bioinformatics Online 1:47–50.

Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology 8:50–59.

Gebhardt, K. J., and L. P. Waits. 2008. High error rates for avian molecular sex identification primer sets applied to molted feathers. Journal of Field Ornithology 79:286–292.

Goodrich, L. J., S. C. Crocoll, and S. E. Senner. 1996. Broad-winged Hawk (*Buteo platypterus*), no. 218. *In* A. Poole and F. Gill [eds.], The birds of North America. Academy of Natural Sciences, Philadelphia.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal in birds. Annual Review of Ecology and Systematics 13:1–21.

Griffiths, R., M. C. Double, K. Orr, and R .J. G. Dawson. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–1075.

Handel, C. M., L. M. Pajot, S. L. Talbot, and G. K. Sage. 2006. Use of buccal swabs for sampling DNA from nestling and adult birds. Wildlife Society Bulletin 34:1094–1100.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, England.

Hedrick, P. W. 1999. Perspective: highly variable loci and their interpretation in evolution and conservation. Evolution 53:313–318.

Hedrick, P. W. 2005. A standardized genetic differentiation measure. Evolution 59:1633–1638.

Hodson, K. A. 1976. Some aspects of the nesting ecology of Merlin (*Falco columbarius richardsonii*) on the Canadian prairies. M.Sc. thesis, University of British Columbia, Vancouver, British Columbia.

Hogan, F. E., R. Cooke, C. P. Burridge, and J. A. Norman. 2007. Optimizing the use of shed feathers for genetic analysis. Molecular Ecology Resources 8:561–567.

James, P. C., I. G. Warkentin, and L. W. Oliphant. 1989. Turnover and dispersal in urban Merlins *Falco columbarius*. Ibis 131:426–429.

Jenkins, J. M., and R. E. Jackman. 1993. Mate and nest site fidelity in a resident population of Bald Eagles. Condor 95:1053–1056.

Johnson, J. A, K. K. Burnham, W. A. Burnham, and D. P. Mindell. 2007. Genetic structure among continental and island populations of Gyrfalcons. Molecular Ecology 16:3145–3160.

Koenig, W. D., D. Van Vuren, and P. N. Hooge. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends in Ecology and Evolution 11:514–517.

Lehman, R. N., K. Steenhof, L. B. Carpenter, and M. N. Kochert. 2000. Turnover and dispersal of Prairie Falcons in southwestern Idaho. Journal of Raptor Research 34:262–269.

Linkhart, B. D., and R. T. Reynolds. 2007. Return rate, fidelity, and dispersal in a breeding population of Flammulated Owls (*Otus flammeolus*). Auk 124:264–275.

LONGMIRE, J. L., A. W. LEWIS, N. C. BROWN, J. M. BUCKINGHAM, L. M. CLARK, M. O. JONES, L. J. MEINKE, J. MEYNE, R. L. RATLIFF, F. A. RAY, R. P. WAGNER, AND R. K. MOYZIS. 1988. Isolation and molecular characterization of a highly polymorphic centromeric tandem repeat in the family Falconidae. Genomics 2:14–24.

LUKACS, P. M., AND K. P. BURNHAM. 2005. Estimating population size from DNA-based closed capture–recapture data incorporating genotyping error. Journal of Wildlife Management 69:396–403.

MCINTYRE, C. L, D. G. DOUGLAS, AND L.G. ADAMS. 2009. Movements of juvenile Gyrfalcons from western and interior Alaska following departure from their natal areas. Journal of Raptor Research 43:99–109.

MEDRANO, J. F, E. AASEN, AND L. SHARROW. 1990. DNA extraction from nucleated red blood cells. Biotechniques 8:43.

MONK, D. J., AND N. A. FORBES. 2007. Raptor physiology; hematological, p. 278–285. *In* D. M. Bird and K. L. Bildstein [EDS.], Raptor research and management techniques. Hancock House, Blaine, WA.

MORRISON, J. L., AND P. B. WOOD. 2009. Broadening our approaches to studying dispersal in raptors. Journal of Raptor Research 43:81–89.

NIELSEN, Ó. K. 1991. Kynbroskaaldur og áttagatryggð fálka. Náttúrfræðistofnunar 60:135–143.

NESJE, M., AND K. H. RØED. 2000. Microsatellite DNA markers from the Gyrfalcon (*Falco rusticolus*) and their use in other raptor species. Molecular Ecology 9:1438–1440.

NESJE, M., K. H. RØED, J. T. LIFJELD, P. LINDBERG, AND O. F. STEENS. 2000. Genetic relationships in the Peregrine Falcon (*Falco peregrinus*) analyzed by microsatellite DNA markers. Molecular Ecology 9:53–60.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD.

NEWTON, I., AND M. MARQUISS. 1982. Fidelity to breeding area and mate in Sparrowhawks *Accipiter nisus*. Journal of Animal Ecology 51:327–341.

OETTING, W. S., H. K. LEE, D. J. FLANDERS, G. L. WEISNER, T. A. SELLERS, AND R. A. KING. 1995. Linkage analysis with multiplexed short tandem repeat polymorphisms using infrared fluorescence and M13 tailed primers. Genomics 30:450–458.

PARK, S. D. E. 2001. Trypanotolerance in west African cattle and the population genetic effects of selection. Ph.D. dissertation, University of Dublin, Dublin, Ireland.

PEARCE, J. M., AND S. L. TALBOT. 2006. Demography, genetics, and the value of mixed messages. Condor 108:474–479.

PENTERIANI, V., AND M. D. M. DELGADO. 2009. Thoughts on natal dispersal. Journal of Raptor Research 43:90–98.

PRESTON, C. R., AND R. D. BEANE [ONLINE]. 2009. Red-tailed Hawk (*Buteo jamaicensis*), no. 52. *In* A. Poole [ED.], The birds of North America online. Cornell Lab of Ornithology, Ithaca, NY. <http://bna.birds.cornell.edu/bna/species/052doi:10.2173/bna.52> (1 December 2010).

PRUGH, L. R., C. E. RITLAND, S. M. ARTHUR, AND C. J. KREBS. 2005. Monitoring coyote population dynamics by genotyping feces. Molecular Ecology 14:1585–1596.

QUELLER, D. C., AND K. F. GOODNIGHT. 1989. Estimating relatedness using genetic markers. Evolution 43:258–275.

RAYMOND, M., AND F. ROUSSET. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248–249.

REESE, E. C., P. LIEVESLEY, R. A. PETTIFOR, AND C. M. PERRINS. 1996. Mate fidelity in swans: an interspecific competition, p. 118–137. *In* J. M. Black [ED.], Partnerships in birds: the study of monogamy. Oxford University Press, New York.

ROBINSON, S. J., L. P. WAITS, AND I. D. MARTIN. 2009. Estimating abundance of American black bears using DNA-based capture–mark–recapture models. Ursus 20:1–11.

ROSENFIELD, R. N., AND J. BIELEFELDT. 1996. Lifetime nesting area fidelity in male Cooper's Hawks in Wisconsin. Condor 98:165–167.

RUDNICK, J. A., T. E. KATZNER, E. A. BRAGIN, O. E. RHODES, AND J. A. DEWOODY. 2005. Using naturally shed feathers for individual identification, genetic parentage analyses, and population monitoring in an endangered Eastern Imperial Eagle (*Aquila heliaca*) population from Kazakhstan. Molecular Ecology 14:2959–2967.

RUDNICK, J. A., T. E. KATZNER, E. A. BRAGIN, AND J. A. DEWOODY. 2008. A non-invasive genetic evaluation of population size, natal philopatry, and roosting behavior of non-breeding Eastern Imperial Eagles (*Aquila heliaca*) in central Asia. Conservation Genetics 9:667–676.

RUNDE, D. E. 1987. Population dynamics, habitat use and movement patterns of the Prairie Falcon (*Falco mexicanus*). Ph.D. dissertation, University of Wyoming, Laramie, WY.

SLATKIN, M. 1995. A measure of population subdivision based on microsatellite allele frequencies. Genetics 139:457–462.

SONSTHAGEN, S. A., S. L. TALBOT, AND C. M. WHITE. 2004. Gene flow and genetic characterization of Northern Goshawks (*Accipiter gentilis*) breeding in Utah. Condor 106:826–836.

STEENHOF, K., M. R. FULLER, M. N. KOCHERT, AND K. K. BATES. 2005. Long-range movements and breeding dispersal of Prairie Falcons from southwest Idaho. Condor 107:481–496.

SWEM, T., C. MCINTYRE, R. J. RITCHIE, P. J. BENTE, AND D. G. ROSENEAU. 1994. Distribution, abundance, and notes on the breeding biology of Gyrfalcons (*Falco rusticolus*) in Alaska, p. 437–444. *In* B.-U Meyburg and R. D. Chancellor [EDS.], Raptor conservation today: proceedings of the IV world conference on birds of prey and owls, Berlin, Germany, May 10–17, 1992. World Working Group on Birds of Prey and Owls, London.

TABERLET, P., AND G. LUIKART. 1999. Non-invasive genetic sampling and individual identification. Biological Journal of the Linnean Society 68:41–55.

TOLAND, B. R., AND W. H. ELDER. 1987. Influence of nest-box placement and density on abundance and productivity of American Kestrels in central Missouri. Wilson Bulletin 99:712–717.

TURCHIN, P. 1998. Quantitative analysis of movement. Sinauer and Associates, Sunderland, MA.

VALIÈRE, N. 2002. Gimlet: a computer program for analyzing genetic individual identification data. Molecular Ecology Notes 2:377–379.

WAITS, J. L., AND P. L. LEBERG. 2000. Biases associated with population estimation using molecular tagging. Animal Conservation 3:191–200.

WAITS, L. P., AND D. PAETKAU. 2005. Noninvasive genetic sampling tools for wildlife biologists: a review of application and recommendations for accurate data collection. Journal of Wildlife Management 69:1419–1433.

WARKENTIN, I. G., P. C. JAMES, AND L. W. OLIPHANT. 1991. Influence of site fidelity on mate switching in urban-breeding Merlins (*Falco columbarius*). Auk 108:294–302.

WEIR, B. S., AND C. C. COCKERHAM. 1984. Estimating *F*-statistics for the analysis of population structure. *Evolution* 38:1358–1370.

WIENS, J. A. 2001. The landscape context of dispersal, p. 96–109. *In* J. Clobert, E. Danchin, A. Dhondt, and J. D. Nichols [EDS.], Dispersal. Oxford University Press, Oxford, England.

WIENS, J. D, R. T. REYNOLDS, AND B. R. NOON. 2006. Juvenile movement and natal dispersal of Northern Goshawks in Arizona. Condor 108:253–269.

WRIGHT, S. 1951. The genetical structure of populations. Annals of Eugenics 15:323–354.