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PHYLOGEOGRAPHY, POSTGLACIAL GENE FLOW, AND POPULATION HISTORY OF NORTH AMERICAN NORTHERN GOSHAWKS (*ACCIPITER GENTILIS*)

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Abstract.—Climate cycling during the Quaternary played a critical role in the diversification of avian lineages in North America, greatly influencing the genetic characteristics of contemporary populations. To test the hypothesis that North American Northern Goshawks (*Accipiter gentilis*) were historically isolated within multiple Late Pleistocene refugia, we assessed diversity and population genetic structure as well as migration rates and signatures of historical demography using mitochondrial control-region data. On the basis of sampling from 24 locales, we found that Northern Goshawks were genetically structured across a large portion of their North American range. Long-term population stability, combined with strong genetic differentiation, suggests that Northern Goshawks were historically isolated within at least three refugial populations representing two regions: the Pacific (Cascades–Sierra–Vancouver Island) and the Southwest (Colorado Plateau and Jemez Mountains). By contrast, populations experiencing significant growth were located in the Southeast Alaska–British Columbia, Arizona Sky Islands, Rocky Mountains, Great Lakes, and Appalachian bioregions. In the case of Southeast Alaska–British Columbia, Arizona Sky Islands, and Rocky Mountains, Northern Goshawks likely colonized these regions from surrounding refugia. The near fixation for several endemic haplotypes in the Arizona Sky Island Northern Goshawks (*A. g. apache*) suggests long-term isolation subsequent to colonization. Likewise, Great Lakes and Appalachian Northern Goshawks differed significantly in haplotype frequencies from most Western Northern Goshawks, which suggests that they, too, experienced long-term isolation prior to a more recent recolonization of eastern U.S. forests. *Received 26 June 2012, accepted 10 February 2013.*

Key words: *Accipiter gentilis*, Apache goshawk, mitochondrial DNA control region, Northern Goshawk, phylogeography, Pleistocene refugia.

Filogeografía, Flujo Genético Post-glacial e Historia Poblacional de *Accipiter gentilis*

Resumen.—Los ciclos climáticos sucedidos durante el Cuaternario desempeñaron un papel crítico en la diversificación de linajes de aves en Norte América, influenciando de forma considerable las características genéticas de las poblaciones contemporáneas. Para probar la hipótesis de que poblaciones de la especie *Accipiter gentilis* estuvieron aisladas históricamente en múltiples refugios del Pleistoceno tardío, evaluamos la diversidad genética y la estructura poblacional, así como las tasas de migración y señales de demografía histórica usando datos de la región control de la mitocondria. Con base en un muestreo de 24 localidades, encontramos que las poblaciones de *A. gentilis* están estructuradas genéticamente a través de una porción grande de su distribución en Norte América. La estabilidad poblacional a largo plazo, junto con la fuerte diferenciación genética, sugieren que la especie estuvo aislada históricamente en al menos tres refugios poblacionales que representan dos regiones: el Pacífico (Cascades–Sierra–isla de Vancouver) y el Suroccidente (planicie de Colorado y montañas Jemez). En contraste, las poblaciones que experimentaron un crecimiento significativo estuvieron localizadas al suroriente de Alaska y Columbia Británica, y las bioregiones de las islas de montaña de Arizona (Sky Islands), las montañas Rocosas, los Grandes Lagos y los Apalaches. En el caso de Alaska y Columbia Británica, las islas de montañas de Arizona y las Montañas Rocosas, *A. gentilis* probablemente colonizó estas regiones desde refugios circundantes. La casi fijación de muchos haplotipos endémicos en *A. g. apache* (islas de montañas de Arizona) sugiere que ha existido un aislamiento de largo plazo tras la colonización. De manera similar, los *A. gentilis* de los Grandes Lagos y de los Apalaches presentaron frecuencias haplotípicas significativamente diferentes de la mayoría de *A. gentilis* del noroccidente, lo que sugiere que ellos también experimentaron aislamiento por un periodo considerable anterior a la recolonización mas reciente de los bosque del oriente de los Estados Unidos.

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Climate cycling during the Quaternary played a critical role in the diversification of lineages across the Northern Hemisphere (Shafer et al. 2011). During the last North American glacial period (Wisconsin; 110,000–10,000 years ago), the Laurentide Ice Sheet extended across most of Canada, nudging the Cordilleran Ice Sheet, which covered what is now British Columbia (Pielou 1991). Pleistocene climatic oscillations determined floristic patterns across the unglaciated portions of North America (Prentice et al. 2000). In particular, the distribution and extent of forested regions differed from current ranges (Betancourt 1990, Delcourt and Delcourt 1993, Jackson et al. 2000) and likely influenced the evolutionary histories of forest-dependent fauna (Hewitt 1996, 2000; Avise 2000). Historical population dynamics and species biogeography can be inferred by identifying contemporary geographic patterns of genetic lineages. Of particular interest is differentiating effects of contemporary demographic processes like dispersal and range expansion from past vicariant events that resulted in population divergence. Especially informative are studies of widespread species that currently occupy both previously glaciated and unglaciated areas, because such studies can uncover signals of expansion of previously isolated refugial populations into deglaciated areas (Lessa et al. 2003, Sonsthagen et al. 2011). Understanding biogeographic history can guide conservation and management initiatives by revealing contemporary relationships among populations, identifying biodiversity hotspots (Myers et al. 2000), and informing predictions for how changes in climate and habitat may affect the distribution of future populations (Barnosky 2008, Hope et al. 2011).

Recent studies that evaluated the phylogeography of broadly distributed North American species have identified consistent patterns that together indicate regions of glacial-period forest refugia south of the North American Ice Sheets. For example, the Hairy Woodpecker (*Picoides villosus*; Klicka et al. 2011, Graham and Burg 2012) exhibits significant genetic differentiation among eastern–boreal and western North American forests. Mountain Chickadees (*Poecile gambeli*; Spellman et al. 2007) and Brown Creepers (*Certhia americana*; Manthey et al. 2011) both exhibit strong phylogenetic splits between the Sierra Nevada–Cascade region and the Rocky Mountains–Great Basin region. Dusky Grouse (*Dendragapus obscurus*) exhibit a phylogenetic split among populations in the Pacific Northwest, Rocky Mountains, and Southwestern forests (Barrowclough et al. 2004).

Another species likely influenced by glacial period climate, and by forest expansion and contraction, is the Northern Goshawk (*Accipiter gentilis*; hereafter "goshawk"). Goshawks are large, vagile forest raptors with a Holarctic distribution. The North American goshawk (*A. g. atricapillus*) occurs across most forested regions, from Alaska to Mexico, and from the Pacific Coast to the Northern Atlantic and is represented by several subspecies (Squires and Reynolds 1997). The goshawk's preference for forest habitats and wide geographic range make it an ideal model species for testing hypotheses about range expansion, vicariance, and the distribution of late Pleistocene forest refugia. Because colonization of postglacial habitats by goshawks was limited by expansion of forests and their prey, studies of goshawks provide a framework for comparative phylogeography of other forest obligates (Arbogast and Kenagy 2001).

Paleoclimate and paleofloristic studies provide the best evidence for where forest refugia were potentially available for goshawks. Breeding habitats are currently limited to forests and woodlands, but these habitats occur over a wide range of climatic conditions: from cold–dry and cold–wet boreal and sub-boreal mixed conifer forests, to temperate coastal rain forests, to dry–warm interior montane forests, to very dry–warm pinyon–juniper woodlands, to cold–dry and cold–wet eastern deciduous forests (Squires and Reynolds 1997). Because goshawks are forest generalists, we assume that all historical coniferous, deciduous, and mixed coniferous–deciduous forests had the potential to provide the species' refugial habitats.

The degree to which goshawks were historically isolated in forest refugia is questionable, and determining such can be difficult for such a vagile species. Genetic signatures from historical periods can be obscured by contemporary relationships among local populations, which are influenced by temporal and spatial, as well as sex- and age-biased, variation in gene flow. Juvenile goshawks tend to be long-distance dispersers (band recoveries observed as far as 442 km in Arizona; Wiens et al. 2006), whereas adults exhibit high mate and breeding-site fidelity (Detrich and Woodbridge 1994, Reynolds and Joy 2006). Consequently, contemporary goshawks across local breeding areas are likely connected via natal dispersal, which likely homogenizes genetic diversity at the local scale. This pattern was exemplified in Utah goshawks, which showed weak (mitochondrial DNA) to no (microsatellite) structuring across sampling locales (≤450 km apart; Sonsthagen et al. 2004). Likewise, variation in reproductive success suggested a small effective population size (harmonic 13-year average N_e = 37 individuals; range: 10–86) in northern Arizona goshawks, but genetic indices suggested that immigration connects them to a much larger reproductive group (Bayard de Volo et al. 2005, 2008). Similarly, goshawks in North Pacific temperate rainforests appear to be arrayed in a metapopulation dynamic (Sonsthagen et al. 2012).

Here, we examine genetic diversity and structure across a large portion of the goshawk's North America range, using sequence data from the control region of the mitochondrial DNA (mtDNA). We tested whether genetic variation was geographically structured and whether current patterns of genetic structure reflect historical isolation and subsequent range expansion from Late Pleistocene glacial refugia. Faunal remains of goshawks have been found in northeastern Tennessee dating to 19,000 years ago (Guilday et al. 1978), and in central coastal California dating to 35,000 years ago (Compton 1931, Miller and DeMay 1942), which indicates that the species occupied eastern and western U.S. forests during the late Wisconsin period. On the basis of fossil data and paleoclimatic and paleobiology data indicating the location of Late Pleistocene forests (Delcourt and Delcourt 1993, Jackson et al. 2000, Williams et al. 2004), we hypothesize that goshawks occupied at least four North American regions of forest refugia: Eastern, Rocky Mountain, Southwestern, and Pacific. If goshawks were isolated within one or more of these refugia during the last glacial period, we predict that geographic structure among major mitochondrial lineages should correspond to the locations of those occupied refugia, and the timing of demographic expansions should coincide with a period of forest expansion during the Late Pleistocene–Early Holocene transition (12,000–9,000 years ago; Jacobson et al. 1987, Thompson et al. 1993, Williams et al. 2004).

Methods

Sample collection, PCR, and mitochondrial control-region sequencing.—Samples (n = 315; blood and plucked and molted feathers) were contributed by several research and monitoring projects

across much of the goshawk's range in North America (Table 1 and Fig. 1). In most cases, blood and plucked feathers were sampled from breeding adults, but in a few cases (some Wisconsin, Minnesota, Alberta samples) blood or feathers were sampled from nestlings (one per nest, and no adults were sampled from the same nest as the nestling). Blood samples were stored in STE buffer or ethanol, and plucked feathers were stored in paper envelopes. All molted feathers were collected from active nest sites where adults were observed breeding in the year of collection, and only one molted feather per nest site was used for analysis. In the cases where breeding goshawks were trapped at nests, and breast feathers plucked, we used one or two feathers per banded individual. Genomic DNA was isolated from blood using the QIAamp kit (Qiagen, Valencia, California) and from feathers using methods described in Bayard de Volo et al. (2008).

A 450-base-pair (bp) fragment of the mitochondrial (mtDNA) control region (domain I) was amplified following Sonsthagen et al. (2004) with two modifications: polymerase chain reaction (PCR) products were purified using either the mini-prep PCR purification kit (Qiagen) or ExoSap-IT (USB, Cleveland, Ohio), and products were sequenced using ABI's BigDye, version 3, Terminator Cycle Sequencing Kit diluted fourfold on an ABI 3130 Genetic Analyzer (Applied Biosystems, Foster City, California). The number of amplification cycles was increased (99 cycles) for sequencing reactions involving PCR products from molted feathers to increase overall sequencing success. Sequence chromatograms were reconciled in BIO-EDIT, version 7.0.7 (Hall 1999). Haplotypes A–H (AY699828–AY699835), J (JQ794588), K (JQ794595), L (JQ794596), M (JQ794594), T (JQ794601), V (JQ794592), and Z (JQ794590) were previously accessioned. New haplotypes for each population were reamplified, checked for consistency, and accessioned in GenBank (KC662186–KC662196).

Analysis of genetic diversity, population genetic structure, and gene flow.—The number of haplotypes, private haplotypes (occurring in

Table 1. Summary of sampling for Northern Goshawk tissues collected across North America. Blood and feather tissues from sample sites were grouped into regional and then bioregional groups for analysis. Sample sites, number of samples and tissue source, and forest region sampled are indicated.

Bioregional groups [a]	Regional groups	Sample sites	Number of samples	Tissue source [b]	U.S. National Forests, Canadian Forest Districts, and National Parks
SEAK-BC	SEAK-BC	Southeast Alaska	7	B	Tongass National Forest
		British Columbia	3	PF	Kispiox Forest District
Not used	Alberta	Alberta	3	PF	None
CASN-VCIS	Vancouver Island	Vancouver Island	5	PF	Coast Forest Region: N. Island, Campbell River, S. Island
	Cascade-Sierra	Cascades, California	22	MF	Klamath National Forest
		Sierra Nevada, California	16	MF	Modoc, Lassen, Plumas and Tahoe National Forests
Colorado Plateau	Colorado Plateau	Southern Utah	28	B	Dixie, Fishlake, Manti-La Sal National Forests
		Kaibab Plateau, Arizona	34	B	Kaibab National Forest
		Mogollon Rim, Arizona	6	B	Apache-Sitgreaves National Forest
Arizona Sky Islands	Arizona Sky Islands	Arizona Sky Islands and Mexico	25	B, MF	Coronado National Forest (Santa Catalina, Peloncillo, Pinaleno, Patagonia, Huachuca, Chiricahua); Chihuahua, Mexico
Jemez Mountains, New Mexico	Jemez Mountains, New Mexico	Jemez Mountains, New Mexico	12	MF	Santa Fe National Forest
Rocky Mountains	Colorado Rockies	Southern Colorado	15	MF	San Juan and Rio Grande National Forests
		Northern Colorado	19	MF	Medicine Bow-Routt, National Forests
	Northern Utah	Northern Utah	29	B	Ashley and Uinta-Wasatch-Cache National Forestss
	Northern Rockies	Western Montana	10	MF	Beaverhead-Deerlodge National Forest
		Eastern Idaho	8	MF	Caribou-Targhee National Forest
	Rocky Islands	Big Horns, Wyoming	7	MF	Bighorn National Forest
		Black Hills, South Dakota	3	MF	Black Hills National Forest
Great Lakes	Great Lakes	Minnesota	10	PF	Chippewa National Forest
		Wisconsin	24	MF, PF, B	Chequamegon-Nicolet National Forest
		Michigan	3	B	Huron-Manistee National Forest
Appalachians	Appalachians	Pennsylvania	14	B	Allegheny National Forest
		Maryland	3	B	None
		West Virginia	9	B	Monongahela National Forest
Total			315		

[a] SEAK-BC = Southeast Alaska–British Columbia; CASN-VCIS = Cascades–Sierra Nevada–Vancouver Island.
[b] B = blood; PF = plucked feathers; MF = molted feathers.

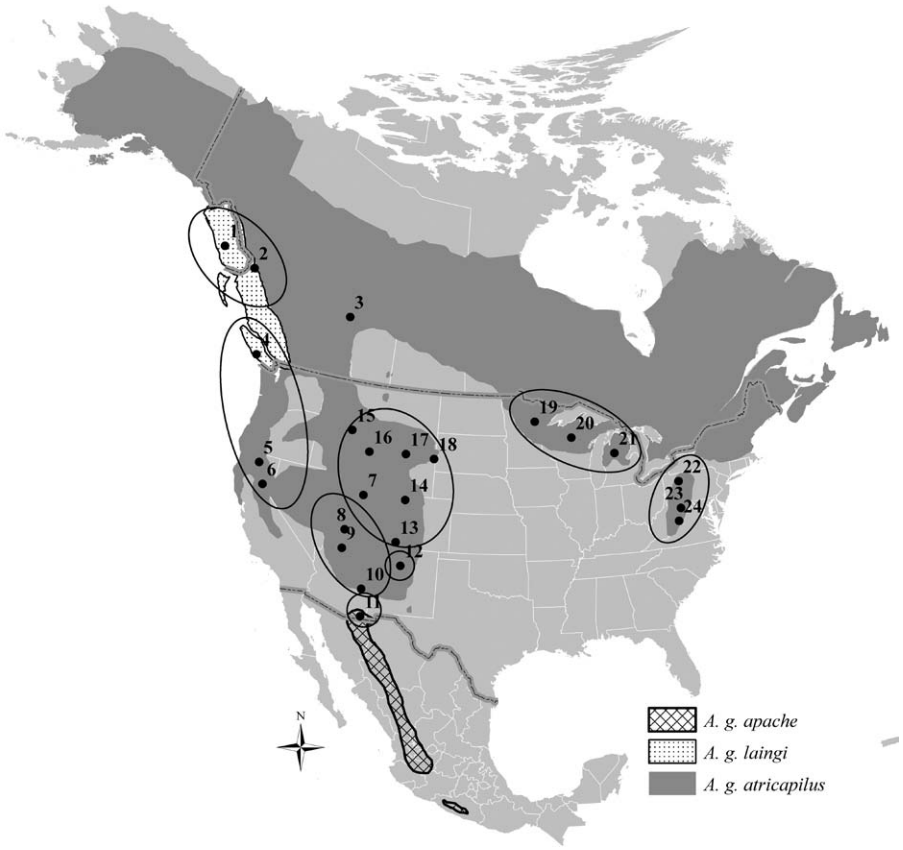

Fig. 1. Geographic range for Northern Goshawks, with numbered sample sites indicated. *Accipiter gentilis laingi* occupies western Canada and southeast Alaska (stippled); sites: (1) Southeast Alaska (n = 7); (2) Coastal British Columbia (n = 3); (4) Vancouver Island (n = 5). *Accipiter g. atricapillus* occupies the majority of the range (gray); sites: (3) Alberta (n = 3); (5) Cascades, California (n = 22); (6) Sierra Nevada, California (n = 16); (7) northern Utah (n = 29); (8) southern Utah (n = 28); (9) Kaibab Plateau, Arizona (n = 34); (10) Mogollon Rim, Arizona (n = 6); (12) Jemez Mountains, New Mexico (n = 12); (13) southern Colorado (n = 15); (14) northern Colorado (n = 19); (15) western Montana (n = 10); (16) eastern Idaho (n = 8); (17) Big Horn Mountains, Wyoming (n = 7); (18) Black Hills, South Dakota (n = 3); (19) Minnesota (n = 10); (20) Wisconsin (n = 24); (21) Michigan (n = 3); (22) Allegheny, Pennsylvania (n = 14); (23) Maryland (n = 3); (24) Monongahela, West Virginia (n = 9). *Accipiter g. apache* occupies southeast Arizona and Mexico (cross-hatched); site: (11) Arizona Sky Islands and Chihuahua, Mexico (n = 25). Circles around groups of sample sites indicate bioregional groups used in analyses.

only one sample locale), and nucleotide (π) and haplotype (h) diversity for each regional group (see Table 1) were calculated in ARLEQUIN, version 3.1.1 (Excoffier et al. 2005). We also used ARLEQUIN to determine nucleotide base frequencies, and transition and transversion rates for the entire North American data set. Evolutionary relationships among haplotypes were assessed using TCS (Clement et al. 2000) to construct a parsimony network.

We assessed population genetic structure using two approaches. First, we tested the hypothesis that goshawks within sample sites fell into broader regional and bioregional groups (Table 1 and Fig. 1) using an analysis of molecular variance (AMOVA) in ARLEQUIN. We combined goshawk sample sites into larger groups based on (1) geographic proximity and (2) possible barriers to gene flow (i.e., the Continental Divide and desert regions). Second, we used ARLEQUIN to evaluate patterns of genetic subdivision by estimating global and pairwise genetic distances (Φ_{ST}) across bioregions (Table 1), applying a Tamura-Nei nucleotide substitution model (Tamura and Nei 1993) as determined using MODELTEST (Posada and Crandall 1998). We also estimated H_{ST}, a measure of global genetic structure, using haplotype frequencies in DNASP, version 4.20.2 (Rozas and Rozas 1999), where equation 2 of Hudson et al. (1992) was implemented. Significance for all global and pairwise estimates was determined by permutation using 1,000 replicates.

We examined gene flow among bioregions by estimating the number of female migrants per generation ($N_f m$) in MIGRATE, version 2.4.2 (Beerli and Felsenstein 1999, 2001; Beerli 2008). We estimated asymmetrical gene flow using full models $\theta(4N_e\mu$ or $N_f\mu)$, where all pairwise gene flow M (m/μ) parameters were allowed to vary and were estimated individually from the data. These were compared with restricted models, where θ and M were equal among bioregions (symmetrical gene flow). MIGRATE runs used maximum-likelihood search parameters, 10 short chains (2,000 trees sampled of 400,000 recorded), five long chains (10,000 trees sampled of 2 million recorded), and five adaptively heated chains (start temperatures: 1, 1.5, 3, 6, and 12; swapping interval = 1). Full

models were run three times and parameter estimates converged. The alternative model was evaluated for goodness-of-fit given the data, using a log-likelihood ratio test (Beerli and Felsenstein 2001).

Demographic history and tests of neutrality.—Patterns of nucleotide diversity that depart from expectations of neutral theory (Kimura 1968) can result from demographic and selective processes. We tested the hypothesis that contemporary goshawks were once isolated within, and have since expanded from, Pleistocene refugia by evaluating whether observed patterns of nucleotide polymorphisms better fit a model of neutral or non-neutral evolution. Program DNASP was used to calculate the expansion coefficient (S/d_k; Peck and Congdon 2004). Comparatively large values indicate recent demographic expansion, whereas smaller values indicate long-term population stability (von Haeseler et al. 1996). We also used DNASP to estimate Fu and Li's (1993) F^* and D^* statistics. Tajima's D (Tajima 1989) and Fu's F_S (Fu 1997) statistics were estimated in ARLEQUIN, as were mismatch distributions and τ, which indicates the number of mutational generations in the past when demographic change occurred. Timing of demographic expansions followed methods outlined in Rogers (1995) using a mutation rate of 14.8% Ma^{-1} for domain I of the control region (Hull and Girman 2005) and a generation time of 3 years (R. Reynolds unpubl. data) to determine whether population expansion coincided with the end of the Wisconsin glaciation (~12,000–10,000 years ago). We note that we have assumed constant rates, and the 3-year generation time approximates an average that varies over time and space (R. Reynolds unpubl. data).

We further tested for fluctuations in historical population demography by evaluating genetic signatures of population growth in LAMARC (Kuhner et al. 1995). LAMARC estimates population growth parameter g, incorporating coalescent theory (parameters: 10 short chains with 200 of 400 sampled trees, and 5 long chains with 20,000 of 400,000 sampled trees). Data were analyzed five times and parameters converged. Positive values of g indicate population growth over time, negative values indicate population decline, and values whose confidence intervals overlap zero indicate population stasis (Waltari and Cook 2005). Because this method incorporates aspects of genealogy, it is sensitive to changes in demography and may have an upward bias (Kuhner et al. 1998). Therefore, we used a conservative estimate of significance based on 99.9% confidence intervals for g to test for significant differences from zero (Waltari and Cook 2005).

Results

Genetic diversity, population genetic structure, and gene flow.—We observed 17 (3.78%) polymorphic sites consisting of 15 transitions, three transversions, and no insertions or deletions. We recovered a total of 26 North American goshawk haplotypes (Fig. 2), 13 of which were private. High haplotype diversity across all populations (h = 0.78) was coupled with low levels of nucleotide diversity (π = 0.003) (Table 2). The number of private haplotypes varied from the highest number in Southeast Alaska–Coastal British Columbia (H_p = 4) to none in the Pacific regions (Vancouver Island, Cascade Sierra) (Table 2). The three Rocky Mountain regions (Colorado Rockies, Northern Rockies, and Rocky Islands) lacked private haplotypes; however, haplotype S was unique to the Rocky Mountain bioregion (Fig. 3).

Table 2. Genetic diversity indices for 12 Northern Goshawk regional groups sampled throughout North America. Regional groups represent larger geographic regions where several sample sites were pooled (see Table 1 for clarification). Number of samples (n), number of haplotypes (H), number of private haplotypes (H_p), nucleotide diversity (π), and haplotype diversity (h) are presented. SD = standard deviation; n/a = non-applicable.

Regional group [a]	n	H	H_p	$\pi \pm$ SD	$h \pm$ SD
SEAK-BC	10	7	4	0.004 ± 0.003	0.87 ± 0.11
Vancouver Island	5	4	0	0.003 ± 0.003	0.90 ± 0.16
Cascade-Sierra	38	4	0	0.002 ± 0.002	0.65 ± 0.05
Northern Utah	29	6	1	0.002 ± 0.002	0.68 ± 0.07
Colorado Plateau	68	8	1	0.003 ± 0.002	0.81 ± 0.03
Arizona Sky Islands	25	5	1	0.002 ± 0.002	0.53 ± 0.11
Jemez Mountains, New Mexico	12	3	1	0.003 ± 0.002	0.62 ± 0.12
Colorado Rockies	34	5	0	0.002 ± 0.002	0.62 ± 0.08
Northern Rockies	18	5	0	0.002 ± 0.002	0.61 ± 0.12
Rocky Islands	10	3	0	0.002 ± 0.002	0.38 ± 0.18
Great Lakes	37	9	3	0.002 ± 0.002	0.58 ± 0.09
Appalachians	26	7	2	0.002 ± 0.002	0.73 ± 0.07
North America	315	26	n/a	0.003 ± 0.003	0.78 ± 0.02

[a] SEAK-BC = Southeast Alaska–British Columbia.

Haplotype B was most frequent (41% of all individuals; Fig. 2), occurring in all North American sites, but was most abundant in the eastern United States (Great Lakes and Appalachians) and across all Rocky Mountain sites (Fig. 3). Haplotype A occurred in 16% of all individuals (Fig. 2), was most abundant in the Cascades and Sierras, and also occurred to the north and across the Intermountain West, but was absent from the Great Lakes and Appalachians (Fig. 3). Haplotype D (11% of all individuals) was also most abundant in the Cascade-Sierras, but occurred in most western U.S. sites and at low frequency within eastern U.S. sites. Haplotype E (9% of all individuals) was dominant in the Arizona Sky Islands (68% within sample) but also occurred in the Colorado Plateau Region and northern Utah, and in one individual from the Appalachians. Haplotype G (6% of all individuals) was dominant in the Jemez Mountains site (58% within sample) but also occurred at low frequency in the Colorado Rockies and the Colorado Plateau, and in a single individual from Lake Tahoe, California (Sierra Nevada site). Haplotype M was prevalent in the eastern U.S. lineage but also occurred in Vancouver Island goshawks.

The AMOVAs of both bioregional and regional groups indicated that ~84% of the variation in haplotype diversity occurred within sites, and ~15% among groups, with very little variation (about 2–4%) among sites within groups (Table 3).

North American goshawks exhibited significant genetic structure (H_{ST} = 0.14, $P < 0.001$; Φ_{ST} = 0.15, $P < 0.001$), with pairwise estimates of Φ_{ST} among bioregions ranging from 0.000 to 0.475 (Table 4). Goshawks in the eastern United States (Great Lakes and Appalachians) were differentiated from those in most of the western bioregions (Φ_{ST} = 0.014–0.418), with the exception of Southeast Alaska–British Columbia. We observed high levels of differentiation between the Arizona Sky Islands and all other bioregions (Φ_{ST} = 0.305–0.475) and between the Jemez Mountains and all other bioregions (Φ_{ST} = 0.142–0.472).

Coalescent gene-flow analyses suggested that gene flow was asymmetrical among sample sites (LnL_{Full} = 92.4, $LnL_{Restricted}$ = –369.0, df = 64, $P < 0.001$). Estimates of $N_f m$ varied across

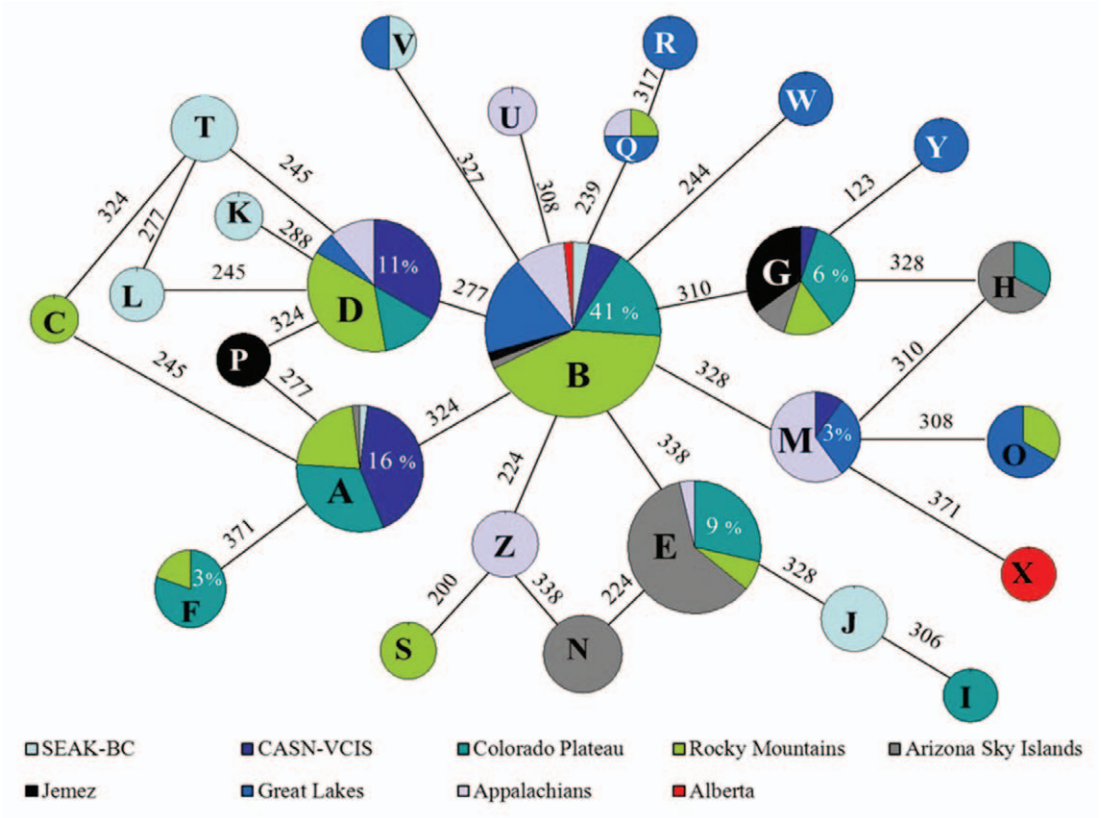

Fig. 2. Parsimony network of mtDNA control-region haplotypes assayed from Northern Goshawks. Each haplotype is identified by capital letters, and each line connecting haplotypes represents a single mutational change occurring at the locus position indicated by the number. Percent values indicate the proportion of all goshawks in our study having that haplotype, with those lacking values occurring at a rate <3%. Color slices indicate the proportional occurrence of that haplotype across bioregions, and circle size indicates the relative number of individuals having that haplotype. SEAK-BC = Southeast Alaska–British Columbia; CASN-VCIS = Cascades–Sierra Nevada–Vancouver Island.

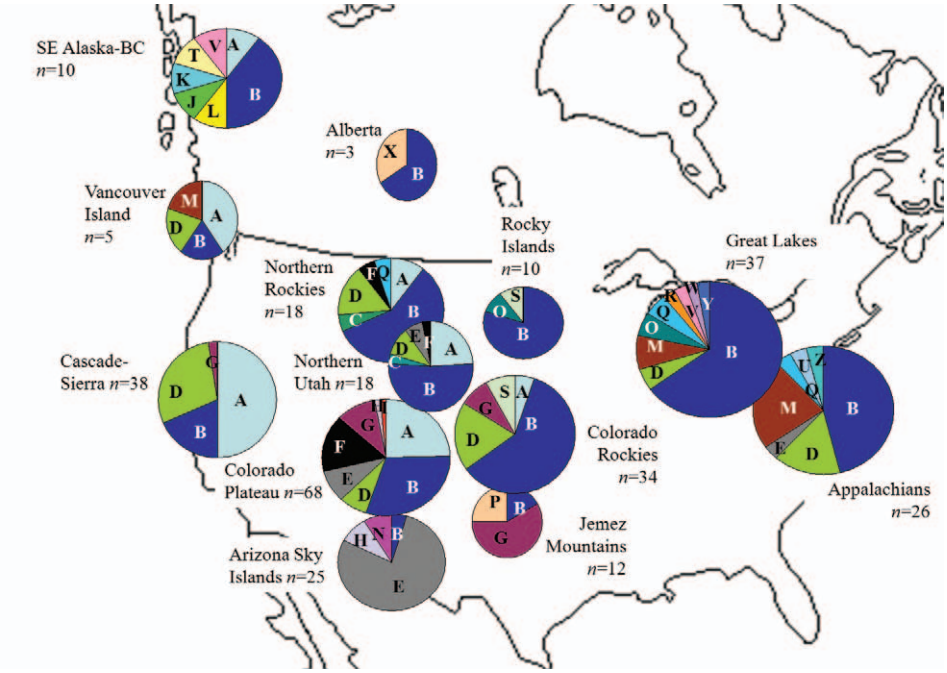

Fig. 3. Geographic distribution and relative frequencies of mitochondrial control-region haplotypes (indicated by capital letters) found in Northern Goshawks sampled across their North American range.

Table 3. Results from a hierarchal analysis of molecular variance, which partitioned variation in mitochondrial control-region haplotype diversity within sample sites, among sample sites within 13 regional or 8 bioregional groups, and among 13 regional or 8 bioregional groups of Northern Goshawks sampled across North America.

Population hierarchy	df	Sum of squares	Variance [a]	Percent variation	Fixation indices	Significance
Among regions	12	37.29	0.09776 V_a	15.63	$\Phi_{CT} = 0.13$	$P < 0.00001$
Among sites within regions	11	8.82	0.01235 V_b	4.45	$\Phi_{SC} = 0.02$	$P = 0.13$
Within sites	296	188.50	0.63683 V_c	85.26	$\Phi_{ST} = 0.15$	$P < 0.00001$
Among bioregions	7	33.23	0.10567 V_a	14.13	$\Phi_{CT} = 0.14$	$P < 0.00001$
Among sites within bioregions	13	10.79	0.01572 V_b	2.10	$\Phi_{SC} = 0.02$	$P = 0.05$
Within sites	290	181.64	0.62634 V_c	83.77	$\Phi_{ST} = 0.16$	$P < 0.00001$

[a] V_a is $\sigma\frac{2}{a} = (\Phi_{CT})\sigma^2$; V_b *is* $\sigma\frac{2}{b} = (\Phi_{ST} - \Phi_{CT})\sigma^2$; V_c *is* $\sigma\frac{2}{c} = (1 - \Phi_{ST})\sigma^2$; $\sigma^2 = \sigma\frac{2}{a} + \sigma\frac{2}{b} + \sigma\frac{2}{c}$.

Table 4. Pairwise genetic distances (Φ_{ST}) for eight Northern Goshawk bioregional populations sampled across North America. Genetic distances (Φ_{ST}) were derived by applying a Tamura-Nei nucleotide substitution model to 450 bp of mitochondrial control-region sequence data. Significant pairwise comparisons ($P < 0.05$) of Φ_{ST} were derived using 1,000 permutations and are indicated in bold.

Bioregions [a]		1	2	3	4	5	6	7	8
SEAK-BC	1								
CASN-VCIS	2	**0.123**							
Colorado Plateau	3	**0.066**	**0.059**						
Arizona Sky Islands	4	**0.315**	**0.475**	**0.305**					
Jemez Mountains, New Mexico	5	**0.168**	**0.217**	**0.142**	**0.472**				
Rocky Mountains	6	0.027	**0.112**	**0.056**	**0.413**	**0.232**			
Great Lakes	7	0.040	**0.232**	**0.123**	**0.418**	**0.283**	**0.047**		
Appalachians	8	0.014	**0.214**	**0.128**	**0.391**	**0.276**	**0.058**	0.000	

[a] SEAK-BC = Southeast Alaska–British Columbia; CASN-VCIS = Cascades–Sierra Nevada–Vancouver Island.

bioregions but ranged from zero to 76 (Table 5), which suggests that gene flow was from the peripheral range into interior sites, and from Rocky Mountain sites into eastern U.S. sites.

Historical demography.—We found comparatively large (>10.0) expansion coefficients (S/d) for the Rocky Mountains and Great Lakes bioregions, but results for all other bioregions were <10.0, which suggests greater demographic stability. Significant estimates of Tajima's D for the Rocky Mountains, Great Lakes, and Appalachian bioregions indicated deviations from mutation–drift equilibrium (Table 6). In all cases, Fu and Li's F^* and D^* were non-significant. Significantly negative Fu's F_S for Southeast Alaska–Coastal British Columbia, Rocky Mountains, Great Lakes, and Appalachians suggested demographic expansion in these regions (Table 6). The small estimate of τ indicated that Arizona Sky Islands goshawks experienced demographic growth much more recently than other sampled bioregions, whereas growth in the Jemez Mountains and Southeast Alaska–Coastal British Columbia occurred more historically (Rogers 1995).

The dating of expansions broadly coincides with the end of the Wisconsin glacial period (approximately 12,000–10,000 years ago) but in some cases extends back to the height of the Wisconsin glacial period (~21,000 years ago), although the 95% confidence limits broadly overlap (Table 6). The Colorado Plateau and Appalachian bioregions had significantly ragged mismatch distributions, which suggests population substructure or multiple population expansions (Table 6). Coalescent modeling indicated historical population growth (g) in the Coastal Alaska–British Columbia, Arizona Sky Islands, Rocky Mountains, Great Lakes, and Appalachians biogregions (Table 6). Growth estimates (g) for Cascades–Sierra Nevada–Vancouver Island, Colorado Plateau, and Jemez Mountains were not significantly different from zero, a result consistent with a pattern of populations located within Pleistocene glacial refugia (Lessa et al. 2003).

Discussion

Evidence of glacial-period refugia and postglacial gene flow.—On the basis of the single mitochondrial gene that we analyzed, we found that both historical isolation and postglacial gene flow shaped the genetic structure of North American goshawk populations. Overall, goshawks exhibited high haplotype diversity across their range (Table 2). As in many North American species (Hull and Girman 2005, Pulgarín-R and Burg 2012), haplotype diversity was characterized by shallow divergence and a star-like phylogeny (Fig. 2), both consistent with rapid population growth and expansion (Slatkin and Hudson 1991, Avise 2000, Ramos-Onsins and Rozas 2002). Coalescent growth estimates (g) that indicate stasis provide evidence of the location of potential refugia, because long-term population stability is associated with mutation–drift equilibrium (Waltari and Cook 2005). We found evidence of demographic stasis (confidence intervals for estimates of g included zero) for the Cascade–Sierra–Vancouver Island, Jemez Mountains, and Colorado

Table 5. Female-mediated gene flow among eight Northern Goshawk bioregional populations, sampled across North America. Estimates were derived in MIGRATE from mitochondrial control-region data, where all pairwise migration parameters varied independently. Estimates of the number of female migrants ($N_f m$ [a]) dispersing per generation are listed for each population pair, with 95% confidence intervals in parentheses. Estimates in bold indicate migration estimates >0.

		Source populations							
θ [b]	Receiving populations [c]	SEAK-BC	CASN-VCIS	Colorado Plateau	Arizona Sky Islands	Jemez Mountains, New Mexico	Rocky Mountains	Great Lakes	Appalachians
0.022 (0.006–0.205)	SEAK-BC	–	**76 (12–1,141)**	**27 (7–541)**	0 (0–89)	0 (0–88)	0 (0–88)	0 (0–88)	0 (0–88)
0.010 (0.009–0.011)	CASN-VCIS	0 (0–0.2)	–	0 (0–0.2)	0 (0–0.2)	0 (0–0.2)	0 (0–0.2)	0 (0–0.2)	**2 (1–4)**
0.008 (0.006–0.011)	Colorado Plateau	**5 (2–14)**	**27 (15–50)**	–	**13 (6–26)**	0 (0–2)	0 (0–2)	0 (0–2)	0 (0–2)
0.011 (0.008–0.015)	Arizona Sky Islands	0 (0–1)	**6 (3–14)**	0 (0–1)	–	0 (0–1)	0 (0–1)	0 (0–1)	0 (0–1)
0.005 (0.003–0.008)	Jemez Mountains, New Mexico	0 (0–2)	0 (0–2)	0 (0–2)	0 (0–2)	–	0 (0–2)	**2 (0.4–8)**	0 (0–2)
0.007 (0.006–0.018)	Rocky Mountains	0 (0–2)	**36 (24–109)**	**4 (2–17)**	0 (0–2)	0 (0–2)	–	0 (0–2)	0 (0–2)
0.008 (0.004–0.015)	Great Lakes	0 (0–6)	0 (0–6)	0 (0–6)	0 (0–6)	0 (0–6)	**15 (5–56)**	–	**59 (24–159)**
0.010 (0.007–0.014)	Appalachians	0 (0–1)	0 (0–1)	0 (0–1)	0 (0–1)	0 (0–1)	**21 (12–73)**	0 (0–1)	–

[a] $N_f m$ = Estimated number of female migrants per generation as determined by the product of θ and M (the rate of migration).
[b] $\theta = N_f \mu$, a composite measure of effective population size and mutation rate. 95% confidence intervals are in parentheses.
[c] SEAK-BC = Southeast Alaska–British Columbia; CASN-VCIS = Cascades–Sierra Nevada–Vancouver Island.

Table 6. Demographic history and mismatch statistics for eight Northern Goshawk bioregional populations sampled across North America. Number of samples (n), Tajima's D; Fu's F_S; mismatch raggedness index (rg); τ (mutational generations since expansion); estimated number of years since demographic expansion; and population growth parameter (g) with 99.9% confidence intervals in parentheses. Statistical significance: $^*P < 0.05$, $^{**}P < 0.01$.

Bioregional group[a]	n	D	F_S	rg	τ	Years since expansion	g
SEAK-BC	10	–1.31	–3.8**	0.08	1.904 (0.475–2.779)	19,297 (3,699–32,919)	2,135** (1,677–2,594)
CASN-VCIS	43	0.23	–0.21	0.13	1.529 (0.223–2.283)	15,497 (0–26,838)	809 (–892 to 2,512)
Colorado Plateau	68	–0.2	–1.41	0.1**	1.459 (1.084–1.889)	14,787 (11,280–19,216)	553 (–71 to 1,178)
Arizona Sky Islands	25	–0.83	–1.00	0.09	0.137 (0.000–2.037)	1,389 (0–23,432)	2,513** (1,518–3,507)
Jemez Mountains, New Mexico	12	1.17	1.32	0.19	3.455 (0.033–4.203)	35,017 (0–63,010)	–105 (–744 to 534)
Rocky Mountains	62	–1.57*	–4.88*	0.07	0.941 (0.654–1.215)	9,537 (6,274–15,517)	1,637** (945–2,329)
Great Lakes	37	–1.77*	–5.52**	0.05	0.99 (0.000–1.996)	10,034 (0–24,547)	2,844** (2,269–3,418)
Appalachians	26	–1.18	–3.2**	0.2**	1.203 (0.688–1.891)	12,193 (4,834–22,723)	4,297** (2,969–5,625)

[a] SEAK-BC = Southeast Alaska–British Columbia; CASN-VCIS = Cascades–Sierra Nevada–Vancouver Island.

Plateau bioregions, which suggests occupancy of goshawks in Pacific and Southwestern refugia. Populations experiencing significant growth (positive estimates of g; Table 6) included those in Southeast Alaska–British Columbia, Arizona Sky Islands, Rocky Mountains, Great Lakes, and Appalachian bioregions. In the case of the latter three bioregions, the timing of growth corresponded to a period of climatic warming and forest expansion during the late Pleistocene–early Holocene transition (13,000–9,000 years ago; Jacobson et al. 1987, Thompson et al. 1993, Williams et al. 2004).

Significant genetic structure (Table 4) among Cascades–Sierra Nevada–Vancouver Island goshawks and all other bioregions suggested that goshawks occupying Pacific refugia

were isolated from other populations during the Wisconsin glacial period. As Late Pleistocene warming fostered the expansion of forests north and east from Pacific refugia south of the Cordilleran Ice Sheet (Barnosky et al. 1987, Pielou 1991), Pacific goshawks apparently also expanded their range into the Rocky Mountains (Table 5). Various taxa used northern dispersal routes, which periodically connected the mesic forests of the Cascades and Northern Rocky Mountains (Carstens et al. 2005). While some species dispersed from the Northern Rocky Mountains into the Cascade forests (*Microtus richardsoni*, *Salix melanopsis*, and *Pinus albicaulis*), goshawks expanded their range from Pacific refugia to the Rocky Mountains, colonizing that region ~10,000 years ago (Table 6). Goshawks also expanded from Pacific refugia north into the Southeast Alaska–British Columbia bioregion (Table 5), where demographic growth dated to ~20,000 years ago (Table 6), a period when the Cordilleran Ice Sheet had not yet retreated from British Columbia. Southeast Alaska's coastal islands (Haida Gwaii; western coast of the outer islands of the Alexander Archipelago) and surrounding areas (Queen Charlotte Sound; Hecate Strait), however, were possibly ice free during the Wisconsin glaciation (Heaton et al. 1996, Carrara et al. 2007). Fossil and genetic evidence indicates that these ice-free areas served as important glacial-period refugia for birds, mammals, conifers, and other plants (Shafer et al. 2010). Our small sample sizes for the Southeast Alaska–British Columbia region, and lack of sampling across Canada and Interior Alaska, precludes us from identifying whether goshawks occupied such coastal refugia. However, the three unique haplotypes identified in our study (Fig. 3), as well as nine other haplotypes (not observed in the present study) identified by Sonsthagen et al. (2012), suggest a post-Pleistocene colonization pattern more complex (Soltis et al. 1997, Shafer et al. 2010) than a simple range expansion from Pacific refugia. Sampling of goshawks from Canadian Boreal, Interior Alaska, and Siberian forests would provide insight on whether goshawks also colonized the Southeast Alaska region from Beringia and Palearctic forest refugia (Shafer et al. 2010).

Goshawk populations in the southwestern United States may have emerged from more than one Southwestern refugium as the Colorado Plateau and Jemez Mountains were genetically differentiated (Table 4), and both had a genetic signature suggestive of population stability (Table 6). Goshawks breeding on the Colorado Plateau exhibited considerable haplotype diversity and significant raggedness (Table 6), which suggests that this area may be one of intermixing from surrounding populations. But five of the eight haplotypes identified there were Southwest-specific (E, F, G, H, I), and the Southern Colorado Plateau and Southwest regions were forested at the height of the Wisconsin period, and into the Holocene (Thompson et al. 1993). This indicates that much of the haplotype diversity of the goshawks on the Colorado Plateau is endemic and that this area served as an important habitat refugium. Likewise, although our sample from the Jemez Mountains site was small, the genetic discontinuity that we identified with the Rocky Mountain bioregion corroborates studies that reported similar phylogenetic breaks in Dusky Grouse (Barrowclough et al. 2004) and American Red Squirrels (*Tamiasciurus hudsonicus*; Arbogast et al. 2001) and suggests that this area may have served as a southern Rocky Mountain refugium.

By contrast, Arizona Sky Island goshawks had a genetic signature of expansion, while showing substantial differentiation from nearby Colorado Plateau and Jemez Mountain goshawks. Today, the Arizona Sky Islands consist of an archipelago of conifer-clad mountains isolated from one another, and from larger forests to the north and south, by expansive deserts. Haplotype diversity for goshawks in the Arizona Sky Islands fits with that expected for an isolated population with a small effective population size. The majority of haplotypes found there (haplotypes E and N) were rare or absent outside that region (Fig. 3), and gene-flow estimates (Table 5) indicate northward expansion only. Thus, the signature of population growth in Sky Island goshawks may reflect expansion of goshawks from pine forests in northwest Mexico. Other forest-dependent species exhibit demographic expansion in northwest Mexico (Ruiz et al. 2010), where forests that were once contiguous with the southern Rocky Mountain forests (in Arizona and New Mexico) became isolated as American Southwest deserts formed during the mid-Holocene (~6,000 years ago; Thompson et al. 1993). The strong genetic differences among Sky Island goshawks and all other populations suggest that goshawks in the extreme American Southwest have been isolated for some time. Additional sampling from goshawks in Mexico would do much to inform us about the role they played in the evolutionary history of goshawks occupying Southwestern refugia.

Evidence supporting occupancy in Eastern refugia was somewhat confounded, because we did not detect a genetic signal of population stability in the Great Lakes or Appalachian bioregions (Table 6). We found significant raggedness for the Appalachian bioregion, which suggests population stasis and/or genetic substructuring resulting from secondary contact of previously isolated lineages. It is highly likely, however, that goshawks occupied eastern U.S. forests during the Wisconsin glacial period. The prevalence of haplotype B, combined with the presence of several unique haplotypes, resulted in significant genetic structure (Table 4) among eastern and most western goshawks. This, combined with the occurrence of faunal remains from an eastern Tennessee cave dating to 19,000 years ago (Guilday et al. 1978), suggests that goshawks occupied Eastern refugial forests during the height of the Wisconsin glacial period.

Broad-scale genetic patterns.—Goshawks are partially sedentary: juveniles tend to disperse from their natal populations, but once they establish a breeding territory they tend to remain (Squires and Reynolds 1997). Although goshawks in northern latitudes irrupt south when Snowshoe Hare (*Lepus americanus*) and Ruffed Grouse (*Bonasa umbellus*) populations decline on 10-year cycles (Mueller et al. 1977, Doyal and Smith 1994), goshawks do not make regular migrations as Cooper's Hawks (*A. cooperi*) and Sharp-shinned Hawks (*A. striatus*) do. Thus, the east–west genetic structure (Table 4) that we found is not entirely surprising and suggests that postglacial gene flow has not been high enough to homogenize haplotype diversity across the goshawk's range.

Among eastern bioregions (Great Lakes and Central Appalachian), goshawks lacked genetic structure (Table 4), a pattern consistent with other eastern–boreal forest birds (Kimura et al. 2002, Klicka et al. 2011) and mammals (Wooding and Ward 1997, Arbogast 1999). Likewise, the patterns of haplotype sharing we found among the Eastern and Rocky Mountain bioregions (the prevalence of haplotype B, combined with the co-occurrence of a few rare haplotypes), is similar to that found for other vertebrate populations (Wooding and Ward 1997, Arbogast 1999, Arbogast et al. 2001, Kimura et al. 2002, Milá et al. 2007). Postglacial floristic

studies show rapid northwestward expansion of conifers from eastern U.S. forest refugia (Jaramillo-Correa et al. 2004, Williams et al. 2004, Godbout et al. 2005). Assuming co-expansion of eastern forest birds and mammals, we expected that our genetic data would reflect expansion of eastern goshawks to the north and west as they tracked their forest habitat and prey (Lundelius et al. 1983). However, gene-flow estimates (Table 5) suggest an opposite trend: Rocky Mountain goshawks expanded into eastern bioregions, a pattern contrary to those found in other phylogeographic studies. It is possible that Pleistocene goshawks moved among Eastern and Rocky Mountain refugia via southern boreal forests that stretched from the eastern United States across the central Great Plains into Kansas (Delcourt and Delcourt 1993) and into Rocky Mountain subalpine conifer forests (Johnson 1975, Wells and Stewart 1987). Alternatively, this pattern of gene flow may result from contemporary immigration of goshawks from Canadian forests. Reviews of field studies and bird atlases (Speiser and Bosakowski 1984, Squires and Reynolds 1997, DeStefano 2005, Postupalsky 2011) indicate that eastern U.S. goshawk populations have increased in recent decades as eastern U.S. forests went through a period of recovery (1950s–1970s; Spahn 1998, DeStefano 2005, Ward et al. 2006). Prior to this time, the goshawk was a rare breeder in eastern U.S. forests, a consequence of severe deforestation, which peaked in the late 19th century (Kennedy 1997, Ward et al. 2006). Moreover, the rapid extinction of the Passenger Pigeon (*Ectopistes migratorius*) likely contributed to the eastern goshawk's decline (Warren 1890, Bent 1937, Schorger 1955, Kennedy 1997, DeStefano 2005). Thus, we may not have actually sampled the goshawks retained in an eastern refugium, which may be better represented by goshawks in Canadian boreal forests.

Contrary to the shared haplotype diversity that we found in the eastern United States, we found genetic subdivisions among all western bioregions. The higher mtDNA structure in the American West may, in part, reflect the fragmented topography in the region, where forested mountains and plateaus are separated by large expanses of desert and shrub-steppe habitats. Juvenile goshawks are known to disperse across these open habitats (Hoffman et al. 2002, Hoffman and Smith 2003, Wiens et al. 2006), but the range of dispersal distances is poorly understood (Squires and Reynolds 1997, Hoffman et al. 2002, Hoffman and Smith 2003). Although these genetic results suggest that goshawks are capable of dispersing great distances, female-mediated gene flow is not extensive across the entire American West. Many vertebrates exhibit genetic structure among western bioregions, including Spotted Owls (*Strix occidentalis*; Barrowclough et al. 1999, 2004; Haig et al. 2004), Dusky Grouse (Barrowclough et al. 2004), and Hairy Woodpeckers and Mountain Chickadees (Spellman et al. 2007). Furthermore, several mammals that are important goshawk preys also exhibit genetic structuring, including red squirrels (*T. douglasii* and *T. hudsinicus*; Arbogast et al. 2001), Northern Flying Squirrels (*Glaucomys sabrinus*; Arbogast 1999), and Tassel-eared Squirrels (*Sciurus aberti*; Lamb et al. 1997). The 15% variation in haplotype diversity explained by our regional or bioregional groupings (Table 3) was significant and was probably driven by the structure among the American West bioregions. Although the amount of diversity explained by our groupings was low compared with that in other sedentary species like the Hairy Woodpecker (Klicka et al. 2011, Graham and Burg 2012) and Brown Creeper (Manthey et al. 2011), it was higher than in the migratory Sharp-shinned Hawk, in which the only substructure supported was an American East and West grouping (Hull and Girman 2005).

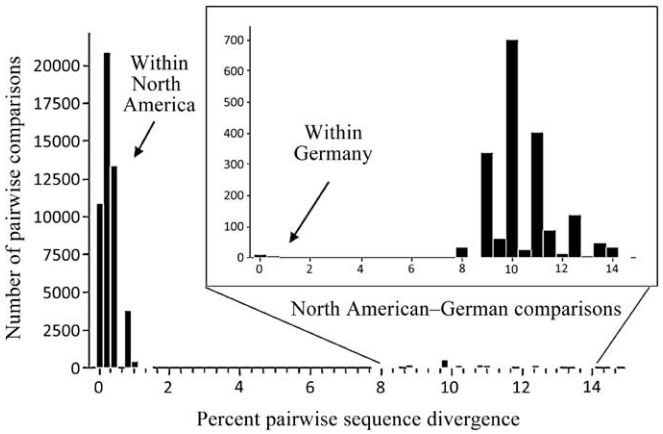

Fig. 4. Pairwise sequence divergence (pairwise distance; mitochondrial control region) among 315 North American (*Accipiter gentilis atricapilus*) and 10 German (*A. g. gentilis*) Northern Goshawks. Birds within North America exhibited little sequence divergence (range: 0–1.3%), whereas sequence divergence among North American and German birds was large (8–14%).

Concluding remarks.—Because we did not analyze samples from the Palearctic range of the goshawk (*A. g. gentilis*), we cannot identify to what degree genetic diversity in North American goshawks was influenced by range expansion of Palearctic populations. To provide perspective, we have included results (Fig. 4) from a previous analysis (Bayard de Volo 2008) of 10 goshawks from Germany for the same mtDNA control-region sequence used herein (KC662197 and AB436743, the latter also found in goshawks from Japan, Russia, Ukraine, and Uzbekistan by Takaki et al. [2008]). Results indicate that although pairwise sequence divergence among goshawks within continents ranges from zero to 1.3%, pairwise sequence divergence among German and North American goshawks ranged from 8% to 14%, lending support to the hypothesis that haplotype diversity in North American goshawks is endemic.

Our conclusions are based on a single genetic marker, and additional analyses, including nuclear genetic markers, will better clarify interpopulation relationships, especially for Arizona Sky Island goshawks. Because mtDNA is haploid and maternally inherited, its effective population size is one-fourth that of nuclear genetic markers, making the rate at which haplotypes geographically sort much faster (Ballard and Whitlock 2004). For species whose populations are isolated over short time scales, geographic structure of mtDNA lineages is expected to be higher than that from nuclear lineages (Zink and Barrowclough 2008). Thus, the high degree of haplotype structure reported here may differ from results based on nuclear genetic markers (Sonsthagen et al. 2004, 2012).

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