Spring 2010

Phylogeography and landscape genetics of the Flammulated Owl: Evolutionary history reconstruction and metapopulation dynamics

Markus Mika
University of Nevada, Las Vegas

PHYLOGEOGRAPHY AND LANDSCAPE GENETICS OF THE FLAMMULATED OWL: EVOLUTIONARY HISTORY RECONSTRUCTION AND METAPOPULATION DYNAMICS

by

Markus Mika

Bachelor of Science
Brigham Young University, Provo
1995

Master of Science
Brigham Young University, Provo
2003

A dissertation submitted in partial fulfillment of
the requirements for the

Doctor of Philosophy in Biological Sciences
School of Life Sciences
College of Science

Graduate College
University of Nevada, Las Vegas
May 2010

UNLV
UNIVERSITY OF NEVADA LAS VEGAS

THE GRADUATE COLLEGE

We recommend the dissertation prepared under our supervision by

Markus Mika

entitled

Phylogeography and Landscape Genetics of the Flammulated Owl: Evolutionary History Reconstruction and Metapopulation Dynamics

be accepted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy in Biological Sciences
School of Life Sciences

Brett R. Riddle, Committee Chair

John Klicka, Committee Co-chair

Dan B. Thompson, Committee Member

Marcos Pérez-Losada, Committee Member

Stephen M. Rowland, Graduate Faculty Representative

Ronald Smith, Ph. D., Vice President for Research and Graduate Studies
and Dean of the Graduate College

May 2010

ABSTRACT

Phylogeography and Landscape Genetics of the Flammulated Owl: Evolutionary History Reconstruction and Metapopulation Dynamics

by

Markus Mika

Dr. Brett Riddle, Examination Committee Chair
Professor of Biological Sciences
University of Nevada, Las Vegas

Dr. John Klicka, Examination Committee Co-Chair
Adjunct Professor of Biological Sciences
University of Nevada, Las Vegas

Taxa occur across ever changing landscapes on different spatial and temporal scales. Choosing the appropriate scale for collecting data and drawing inferences is critical for understanding the history of a species and its populations. Here, I describe research in which I investigated phylogenetic patterns and population genetics for Flammulated Owls (*Otus flammeolus*) representing 14 localities from throughout the species' distribution, and compared regional landscape features with the distribution of genetic diversity. This small, insectivorous owl migratory (Family Strigidae) breeds in western conifer and deciduous dry forests of the mountains from southern Mexico to British Columbia. Sedentary populations are found in the southern Sierras of Mexico within the Transvolcanic Belt whereas all other populations are presumed to be migratory. Among all sampled localities, one population from northeastern Mexico

showed genetic differentiation and reduced gene flow from all others. High levels of gene flow among all other populations confirm anecdotal evidence of significant natal dispersal. The only sedentary population (southwestern Mexico) did not exhibit separation from populations in Canada and the United States. Low genetic variation in that locality is likely due to a recent expansion from the north or a prolonged genetic bottleneck. Several localities throughout the distribution showed high levels of genetic diversity, frequently combined with large proportions of private haplotypes, indicating long-term population stability. Previously uncovered palaeoecological evidence of flora associated with Flammulated Owl habitat in the southern and northern Rocky Mountains is consistent with the high levels of genetic diversity recovered for owls in this region. On a landscape genetic level, current measures of population sizes, territory density estimates obtained in the field, and habitat suitability averages calculated from ecological niche modeling were good predictors of nucleotide diversity. A patch proximity metric showed a very strong positive relationship with current population sizes in the absence of genetic variables. The results indicated that metapopulation dynamics among habitat patches of various sizes, habitat quality, and population densities are important in shaping genetic diversity and distributions in this species.

ACKNOWLEDGMENTS

First and foremost I would like to thanks my advisor, Dr. John Klicka, for allowing me to work on this difficult taxon, providing me with all the necessary support, and continuously encouraging me to improve my work. I thank Dr. Brett Riddle, Dr. Marcos Pérez-Losada, Dr. Dan Thompson, and Dr. Stephen Rowland for their continuous interest in my study and my professional development. Their comments have significantly improved my dissertation manuscript, for which I am grateful. Garth Spellman introduced me to all the necessary techniques for efficient processing of genetic samples in the laboratory. He also provided me with a lot of background on complicated methods of analysis, and helped in the field during expeditions to Mexico. Stacy Mantooth and Derek Houston constantly encouraged me in my professional progress and helped me tremendously to understand analytical software. Jeff DaCosta was a valuable assistant throughout many of my field trips and his raw talent as field biologist is extremely rare. Brian Smith encouraged me consistently throughout our collaboration and was instrumental in achieving success during my most important field trip to Mexico. He also introduced me to various analytical software with great enthusiasm and provided helpful and thorough comments on earlier manuscripts of this document. Jeremy Batten, Connie Herr, Adam Leland, Tereza Jezkova, Vicky Hemmings, Sean Neiswenter, and other members of the UNLV Systematics group also provided help and encouragement throughout the years. I would like to thank my collaborators in Mexico working for the Colección Nacional de Aves at the Universidad Nacional Autónoma de México (UNAM) and the Universidad Autónoma de Nuevo León (UANL). They tirelessly organized and

participated in our field explorations: Dra. Patricia Escalante (UNAM), Marco Gurrola Hidalgo (UNAM), Noemi Chávez Castañeda (UNAM), Ricardo Canales (UANL), Irene Ruvalcaba Ortega (UANL). This research was funded in part through grants from the Marjorie Barrick Museum, the Graduate College and Graduate and Professional Student Organization (GPSA) at UNLV, the Frank M. Chapman Memorial Fund for graduate research at the American Museum of Natural History (AMNH), the United States Forest Service (USFS), and the Nevada Department of Wildlife (NDOW). I am eternally grateful to my father Heinz Mika, who instilled in me an interest in the natural world and the drive to teach others about its beauty. And most importantly, I want to thank my wife, Teresa, for her unwavering support and acceptance of my humble being and her love for our son Samuel Charles.

TABLE OF CONTENTS

ABSTRACT iii

ACKNOWLEDGEMENTS v

LIST OF TABLES viii

LIST OF FIGURES ix

CHAPTER 1 POPULATION GENETICS AND EVOLUTIONARY HISTORY OF THE FLAMMULATED OWL (*OTUS FLAMMEOLUS*) 1
- Abstract 1
- Introduction 3
- Materials and Methods 8
- Results 16
- Discussion 23

CHAPTER 2 LANDSCAPE-MEDIATED DISTRIBUTION OF GENETIC DIVERSITY IN THE FLAMMULATED OWL (*OTUS FLAMMEOLUS*) 47
- Abstract 47
- Introduction 48
- Materials and Methods 51
- Results 57
- Discussion 59

CHAPTER 3 CONCLUSION 71

LITERATURE CITED 75

APPENDIX SPECIMEN DATA 99

VITA 105

LIST OF TABLES

Table 1.1 Diversity statistics for population localities 31
Table 1.2 Amova analysis under Samova design with predetermined group number (K) of three 32
Table 1.3 Estimates of selective neutrality (*D* and F_s) and raggedness (*R*) of mismatch distributions 33
Table 1.4 Bioclimatic variables used in the ecological niche modeling software package Maxent 34
Table 1.5 Summary of Maxent results at common threshold levels averaged over three runs 35
Table 2.1 Observations and estimates of dependent and independent variables for linear regression models 64
Table 2.2 General Linear Model statistics with nucleotide diversity estimate (π) from 12 localities as dependent variable 65

LIST OF FIGURES

Figure 1.1 Median-joining haplotype network with geographic color coding along north-south axis 39
Figure 1.2 Semi-log regression plot of genetic distance over geographic distance (Slatkin 1993) 40
Figure 1.3 Regression curve and 95% confidence interval contrasting proportion of private haplotypes and Θ_k 41
Figure 1.4 Frequency plots of effective population size Θ and migration rate M for all Canada and United States localities combined in comparison to Nuevo León 42
Figure 1.5 Select mismatch distributions for a pooled group, northern Utah, southern New Mexico, and Nuevo León 43
Figure 1.6 Bayesian skyline plot tracking changes in median effective population size through the recent history of the Flammulated Owl 44
Figure 1.7 Extrinsic receiver operating characteristics (ROC) curves from test, training, and random model predictions and affiliated AUC values 45
Figure 1.8 Estimates of suitable habitat for the Flammulated Owl predicted from transferral of ecological niche model under palaeoclimatic conditions 21 kya 46
Figure 2.1 ImageJ graph used for patch size, isolation, and proximity estimates 67
Figure 2.2 Partial residual plot for habitat suitability estimate predicting population sizes in the presence of proximity metrics and territory density estimates 68
Figure 2.3 Simple regression plot of nucleotide diversity (π) compared with integrated independent variable of population size 69
Figure 2.4 Partial residual plots of territory density and habitat suitability compared with nucleotide diversity (π) 70

CHAPTER 1

POPULATION GENETICS AND EVOLUTIONARY HISTORY OF THE FLAMMULATED OWL (*OTUS FLAMMEOLUS*)

Abstract

In this study, I investigated phylogenetic patterns and population genetics using the mitochondrial marker ATPase 8 and 6 for Flammulated Owl (*Otus flammeolus*) specimen from 14 localities, while considering phylogeographic and climatic characteristics of the region. This small, insectivorous owl (Family Strigidae) breeds in western conifer and deciduous dry forests of the mountains from southern Mexico to British Columbia. Sedentary populations are found in southern Mexico along the Transvolcanic Belt. Among all sampled localities, only one population (Nuevo León, Mexico) showed genetic differentiation and reduced gene flow with respect to all other populations. Extended spatial isolation of northeastern Mexican habitat appeared as the most likely explanation for this pattern. High levels of gene flow among all other populations confirmed anecdotal evidence of significant natal dispersal. The only sedentary population (southwestern Mexico) did not exhibit separation from populations in Canada and the United States. Low genetic variation in that locality was likely due to a recent expansion from the north or a prolonged genetic bottleneck. Several localities throughout the distribution showed high levels of genetic diversity, frequently combined with large proportions of private haplotypes, indicating long-term population stability. Previously uncovered palaeoecological evidence of flora associated with Flammulated

Owl habitat in the southern and northern Rocky Mountains is consistent with the high levels of genetic diversity recovered for owls in this region. The results of this study conflicted with the distribution of the species during the last glacial maximum as suggested by ecological niche models. Their outcome proposed a historical distribution in the southern Cascade and Sierra Nevada mountain ranges and along the Mogollon Rim (Arizona) with a subsequent range expansion in a northeastern direction.

Introduction

Our knowledge on the phylogeography of many North American bird species is still lacking (Milá et al. 2007) and reconstructions of population history remain unresolved for most Nearctic owl species (Order Strigiformes). These secretive taxa not only occur in low densities, as is expected for raptors, but their nocturnal behavior and cryptic plumage (del Hoyo et al. 1999) create difficulties in obtaining adequate sample sizes to study intraspecific genetic variation. Although elusive, the insectivorous Flammulated Owl (*Otus flammeolus*) is one of the most common owls throughout dry and open forests in the mountains of western and southern North America (McCallum 1994a; Oleyar et al. 2003). A partial migrant, breeding populations from northern Mexico to British Columbia are believed to winter along the Mexican Transvolcanic Belt (TVB). Non-migratory residents breed from the southern tip of the Sierra Madre Occidental across the southern mountain ranges into northwestern Oaxaca, Mexico. Breeding habitat, where the species nests in tree cavities excavated by woodpeckers (McCallum 1994a), consists of mature, open, and dry mixed conifer forests associated with Douglas-fir (*Pseudotsuga menziesii*), Yellow Pine (*Pinus ponderosa* & *Pinus jeffreyi*), Engelmann Spruce (*Picea engelmannii*), White Fir (*Abies concolor*), and Subalpine Fir (*Abies lasiocarpa*) (Linkhart 1984). A strong association with the mature deciduous Quaking Aspen (*Populus tremuloides*), which often provides nest cavities in food resource rich environments (Mika 2003), has been described in recent years (Marti 1997).

Packrat midden and lake core sample data have produced evidence of historical localities of flora affiliated with Flammulated Owls in several regions across the American west (Van Devender et al. 1984; Weng and Jackson 1999). Mountain ranges of northern California and southern Oregon are considered floristic hotspots for high conifer species diversity (Briles et al. 2008). Lake core samples from the Siskiyou Mountains confirmed high conifer diversity during the late glacial maximum (~17 - 15 kya) including some species affiliated with Flammulated Owl habitat (West et al. 2007). On a larger scale, Douglas-fir pollen samples from the last glacial maximum (LGM; ~21 kya) were restricted to the southern half of the Sierra/Cascade ranges and 'virtually absent on the Pacific slope of Washington and Oregon' (Bartlein et al. 1998). Genetic variation in allozyme data provided equivocal results pertaining to the existence of interiour Douglas-fir refugia during the LGM. A refugium was suggested for southeastern Idaho and northern Utah (Li 1986), but the level of cold tolerance in this trees species (Rehfeldt 1978) may indicate a wider distribution during the LGM than previously inferred (Brunsfeld et al. 2001). Douglas-fir and Ponderosa Pine refugia were found in woodrat middens during the full-glacial period in the mountains of the northern Chihuahuan desert in southern New Mexico (Van Devender 1990) extending south towards Big Bend, Texas. A second Ponderosa Pine refugia was detected at the southern extent of the Sierra Nevada range and both locations were confirmed by two current genetically distinct eastern and western groups of Ponderosa Pine that have expanded northward since the LGM (Latta and Mitton 1999). Less information is available on post-glacial presence of Quaking Aspen, but records from the early Holocene place its pollen in the southern Lake Agassiz

Basin in North Dakota (Strong and Hills 2005; Yansa and Ashworth 2005). The flora affiliated with the Flammulated Owl has changed during the late Pleistocene, but the extent of the habitat shifts is not entirely clear.

A multitude of phylogeographic patterns at numerous temporal scales have been documented among co-distributed taxa (Ball and Avise 1992; Bermingham and Moritz 1998). This temporal variation has been fueling the debate on the major mechanisms of intraspecific avian diversification (Avise and Walker 1998; Klicka and Zink 1997; Lovette 2005). Unique ecological niches, which have undergone temporal and spatial shifts themselves are obvious factors responsible for some of the diversification (Ohlson et al. 2008). However, initial levels of genetic variability, maintenance or loss of genetic homogeneity among populations due to high or low levels of gene flow respectively, and drastic changes in allele frequencies through genetic drift have left their mark on distribution patterns of bird species (Zink 1996). Current intraspecific patterns of North American avian taxa can be traced through more recent events during and after glacial cycles of the late Pleistocene (Burg et al. 2005; Cracraft 1982; Hewitt 2000; Jones et al. 2005; Mengel 1970; Rand 1948) all the way back to the late Pliocene (Klicka and Zink 1997).

Intraspecific divergence may be attributed to various sources, but will result in similar expectations reflected in the genetic structure. For instance, the White-breasted Nuthatch (*Sitta canadensis*) was believed to have diverged into four major monophyletic clades, which was most likely cause by late Pliocene aridification and Rocky Mountain uplifts (Spellman and Klicka 2007). On a very different temporal and spatial scale, the

evolution of isolated migration routes or wintering grounds have been shown to play a role in causing divergence among populations of the Swainson's Thrush (*Catharus ustulatus*) and Wilson's Warbler (*Wilsonia pusilla*), two passerine species with eastern and western representatives (Clegg et al. 2003; Ruegg et al. 2006). Genetic data for both species revealed a leap-frog pattern of migration, where migrants from more northern breeding sites would winter further south in the tropics than their counterparts from southern breeding grounds in North America. Multiple late Pleistocene refugia have been responsible for intraspecific divergence in the case of the Tawny Owl in Europe (Brito 2005). Populations pushed into Mediterranean peninsular regions still bear signals of separation even after ecological release and northward expansion during the last 18 kya. Migratory species with disjunct populations may have experienced divergence regardless of their mobility. In the MacGillivray's Warbler (*Oporornis tolmiei*) a small and remote population in northeastern Mexico not only has separated from their northern conspecifics genetically, but it was also unaffected by demographic post-glacial expansion observed in the north (Milá et al. 2000). The expectations of divergence in these cases are structured gene trees or population subdivision, high genetic variation among clades, reduced or absent gene flow between clades, and a lack of recent demographic expansion across all samples, albeit expansion within clades is still possible. In contrast, populations may have been prevented from diverging given a unique set of circumstances. The Pygmy Nuthatch (*Sitta pygmaea*) experienced sudden postglacial northern and southern expansions from a single refugium with a more homogeneous genetic signature and lack of structure throughout its distribution

(Spellman and Klicka 2006). Panmixia was observed throughout populations of the North American Tree Swallow (*Tachycineta bicolor*) having accumulated genetic diversity over time, but lacking phylogenetic structure due to continuous gene flow across populations (Stenzler et al. 2009). The genetic expectations for expansions from single refugia or panmixia are shallow unstructured gene trees, low variation among all samples for the single refuge hypothesis, but high genetic variation in panmixia. Migratory bird species from temperate zones feature a wide spectrum of phylogeographic patterns depending on the level of shared evolutionary history (Zink 1996), demography, and distributional constraints (Bermingham and Moritz 1998).

To compare responses of the Flammulated Owl to the history of its range, I investigated phylogeography and demographic changes of the species as described by mitochondrial DNA (mtDNA). Populations across the distribution may exhibit divergence from each other or lack significant structure based on aforementioned scenarios and expectations. I used phylogenetic and population genetic analyses to contrast observations in this owl species to expectations under any given scenario and address the following: First, I applied phylogenetic analysis to evaluate genetic structure in the Flammulated Owl, paying particular attention to possible breaks between migratory and non-migratory populations. Second, I used coalescent approaches in population genetics to measure levels of gene flow persisting between populations. Third, I assessed demographic changes over evolutionary time to detect population fluctuations triggered by historical events across the distribution. Finally, I investigated the distribution of genetic diversity across all localities. More specifically, given the propensity of some

neotropical migrants to display lower genetic diversity in northern populations due to recent northward expansions (Milá et al. 2006), I was interested if genetic diversity in Flammulated Owls was negatively correlated with latitude as well. The lack of understanding of recent evolutionary history in the order Strigiformes combined with variable migratory behavior make the Flammulated Owl a compelling taxon for investigation.

Materials and Methods

Sample summary

I obtained genetic samples from 163 individuals from 14 different localities (see Appendix I). Samples were collected from throughout the species distribution, and included migratory populations from the northern extent of the range and permanent residents from southern Mexico. In all regions, I collected ≥ 10 individuals to include adequate sample sizes for populations genetic analyses (Harding 1996; Morando et al. 2003).

Sample collection

Due to the migratory nature of *O. flammeolus*, genetic samples were obtained only within or near breeding territories. Two population samples, one from northern Utah and the other from western New Mexico came from previous breeding studies of the species in these localities (Arsenault et al. 2002; Mika 2003). Those birds were captured at known nest sites located in cavities or man-made nest boxes and were subsequently released at the same location. I captured most individuals using a male territorial

playback call and a single mist net at locations deemed suitable during preliminary daytime surveys. A major criterium of survey site selection was a high number of available perching opportunities at relatively low heights (up to seven meters maximum), usually located along forest edges and clearings. I then processed each bird at the location of capture and collected one inner secondary flight feather and one second central tail feather to use in DNA extraction. Photos of the bird's front, back, facial disk, and from the upper and lower side of the right wing were recorded for each individual and will be included as digital vouchers at the Marjorie Barrick Museum of Natural History (MBM) at the University of Nevada Las Vegas (UNLV). A single sample from the Colección Nacional de Aves at the Instituto de Biología UNAM (CNAV) in Mexico City was obtained to supplement the most southern population in Michoacán. A subsample of voucher specimens were collected from populations in Nevada, Arizona, and Mexico.

Laboratory techniques

Total genomic DNA for all specimens was extracted from feather and tissue samples using standard protocols found in the DNeasy Tissue Kit (Qiagen, Valencia CA). For all feather samples, I supplemented the initial incubation solution with 30 µl of Dithiothreitol (DTT) to dissolve the sheath of the feather calamus. I amplified and sequenced 829 base pairs of the adjacent genetic markers ATPase 8 and 6 (ATPase) from the mitochondrial genome (mtDNA) for all 163 individuals using the primers CO2GQL (5'-GGA CAA TGC TCA GAA ATC TGC GG-3') and CO3HMH (5'-CAT GGG CTG GGG TCR ACT ATG TGH-3') (Greenberg et al. 1998; Joseph et al. 2003). PCR reactions of 12.5 µl were prepared and executed under the following amplification conditions:

initial 10 minute denaturation at 94ºC followed by 40 cycles of 94ºC for 30s (denaturation), 54ºC for 45s (annealing), and 72ºC for one minute (elongation). Finally, a 10 minute extension phase was followed by a 4ºC soak. Successful amplifications were purified using the Exosap-IT (USB Corporation) purification following a heating protocol of 15 minutes at 37ºC with a subsequent phase of 15 minutes at 80ºC. Sequencing reactions of 20 µl were performed using Big Dye Terminator v3.1 (Applied Biosystems) and purified with a magnetic bead cleanup (Agencourt Biosciences). Sequences were analyzed on an ABI 3100-Avant automated sequencer (Applied Biosystems). Sequences were aligned and verified by eye using Sequencher 4.8 (Gene Codes Corporation) and checked for anomalies (Numts) (Sorenson and Quinn 1998) by comparing them to genomic mtDNA of the Barred Owl (*Strix varia*).

Molecular calibration

The molecular clock calibration employed was based on a recent multilocus treatment of Old World Scops-owls (Fuchs et al. 2008), a putative sister clade to the New World Screech-owls. Their dates were calibrated with an owl fossil (subfamily Asioninae) from the early Miocene (Mlíkovský 1998) and the formation date of Grand Comoro Island (Emerick and Duncan 1982) some 0.5 million years ago (mya). I combined the ATPase 6 data from Fuchs et al. (2008) with Flammulated Owl data for a total of 22 individuals. These data were used to estimate the timing of the split between the Flammulated Owl and four closely related New World Screech-Owls (*Megascops kennicottii, M. trichopsis, M. guatemalae,* and *M. cooperi*). An HKY +I +G model of sequence evolution was indicated (jModeltest, Posada 2008) and the model-corrected

data were analyzed using the program Beast (Drummond et al. 2005). The calibration points used by Fuchs et al. (2008) including 95% confidence intervals (C.I.) were used to calibrate several nodes. Results were then scaled to uncorrected distances for markers ATPase 8 & 6. The uncorrected rate of divergence estimated for ATPase 8 & 6 used in subsequent analyses was calculated at 2.39% per million years. Consequently, a per lineage mutation rate (μ) of 1.195×10^{-8} was implemented in subsequent analyses.

Phylogenetic analysis

To estimate the model of nucleotide substitution in my samples I used likelihood calculations carried out in an integrated version of Phyml (Guindon and Gascuel 2003) followed by sequential likelihood ratio test methods under the Bayesian Information Criterion (BIC) (Schwarz 1978). Both steps are implemented in the software package jModeltest 1.01. The suggested model was used in all subsequent genetic population analyses. Genetic relationships of haplotypes were visualized by means of a median-joining network using the programs Network 4.5 (Bandelt et al. 1999) and statistical parsimony using TCS 1.18 (Clement et al. 2000).

Genetic differentiation and population structure

The program DnaSP 4.0 (Rozas et al. 2003) was used to obtain nucleotide and haplotype diversity indices among samples (Nei 1987; Nei and Li 1979; Tajima 1983). To obtain a measure of genetic differentiation between population samples, I computed pairwise comparisons for both the fixation index F_{ST} (Hudson et al. 1992b; Wright 1969) using the Arlequin 3.1 software program (Excoffier et al. 2005) and genetic distance G_{ST} (Hudson et al. 1992a; Nei 1973) using DnaSP. Unlike F_{ST} distance methods, G_{ST}

estimates are less affected by bias connected to having small mitochondrial samples (Barrowclough et al. 2006). A transformed value of pairwise genetic distance [$G_{ST}/(1-G_{ST})$] was carried over into a regression analysis to calculate isolation-by-distance (IBD) among surveyed populations (Holsinger and Mason-Gamer 1996; Rousset 1997; Slatkin 1993). Analysis of molecular variance (AMOVA) among all population samples was executed in Arlequin (Excoffier et al. 1992). This technique was extended using the program Samova 1.0 (Dupanloup et al. 2002) to include spatial data on sample locations without *a priori* assumptions regarding population structuring. This approach operates under a simulated annealing procedure to maximize the F_{CT} differentiation values among groups. The number of groups was chosen based on the largest, still significant F_{CT} obtained from the program (K. Zamudio, pers. comm.). Significance values were tested using 1023 permutations over variance and fixation indices. In addition, I carried out an examination of population history and gene flow by running an automated version of nested clade phylogenetic analysis (NCPA) as implemented in the program ANeCA 1.0.1 (Panchal and Beaumont 2007).

To provide an approximation of intra-population diversity, proportions of private haplotypes, i.e. those found exclusively in one specific sampling location were calculated for each population. These values are shown to be correlated with levels of isolation and frequency of migration from and to other populations if regressed against a measure of effective population size (Θ) from an independent calculation (Helgason et al. 2001). Simple regression analysis was performed including a 95% confidence band over the proportions of private haplotypes and Θ_k calculated from Arlequin (Goodacre et al.

2005). Outlier populations were deemed as either in isolation with reduced levels of migration or clustered with increased levels of migration depending on their position above or below expected values.

Gene flow, N_e, and TMRCA

Migration rates (M), Θ, and time to most recent common ancestor (TMRCA) were estimated in a Bayesian inference framework under the principle of the coalescent (Kingman 1982) using the software package Migrate-n 3.0 (Beerli 2006). Sample sizes for each population were kept equal by randomly reducing samples from the larger population before analysis. I repeated the random sample selection for a total of 10 runs to create multiple unique combinations of individuals in that population. Posterior distributions in Migrate were tested using the Metropolis-Hastings algorithm and exponential prior distribution settings were carried out for M and Θ. Each procedure was run for 40 million generations with a two million step burn-in. A heating scheme of four static chains with temperatures of 1.0, 1.5, 3.0, and 40.0 was applied to the search parameters. Bayesian search parameters from Migrate output logs were tested for adequate trace behavior and sufficient ESS values using the program Tracer 1.4.1. In cases of failed convergence during coalescent analyses, I used F_{ST}-based migration estimates to substitute for missing rates (Nei 1973; Nei 1982).

Demographic history and Bayesian skyline plot

I created mismatch distributions to examine pairwise sequence differences within populations, and calculated the raggedness index *R* (Harpending 1994) to detect signals of stability or expansion over time (Slatkin and Hudson 1991). Neutrality tests computing

Tajima's *D* (Tajima 1989) and Fu's F_s (Fu 1997) values were performed among all sampling locations and tested for significance using coalescent simulations within DnaSP at 5000 generations. Fu (1997) and subsequent simulation analyses by others (Excoffier et al. 2005) have determined a significant level $\alpha = 0.02$ for Fu's F_s.

I investigated the validity of summary estimates on population size changes over time and obtained a second independent estimation of TMRCA under a coalescent approach using the software package BEAST 1.4.8 and its accompanying programs BEAUti 1.4.8 and Tracer 1.4.1 (Drummond et al. 2005). This method implements a Bayesian skyline plot approach (Pybus et al. 2000) utilizing a standard Markov chain Monte Carlo (MCMC) sampling procedure. The results are based on posterior probabilities of effective population sizes (N_e) along a coalescing phylogeny. The Bayesian skyline plot group number of 40 was chosen to obtain a high resolution output under constraints of a strict molecular clock suggested for intraspecific analyses. I performed multiple runs and increased the number of generations to build up final effective sampling sizes (ESS) to a minimum of 200 for all estimated parameters as suggested by the authors of the software (Drummond and Rambaut 2003). This was accomplished using 180 million generations of which 10% were discarded as burn-in. The procedure was then repeated three times using computer resources from the Computational Biology Service Unit at Cornell University to verify the results.

Ecological niche modeling

To build a distribution model for the Flammulated Owl, I used ecological niche modeling (Guisan and Zimmermann 2000) by applying location records to a maximum

entropy method implemented in the program Maxent 3.2.1 (Phillips et al. 2006). Maxent is a machine-learning software package designed to find maximum entropy distributions among climatic variables to predict logistic non-negative probabilities of a target distribution on a presence-only data set (Stockman and Bond 2007). The model for this analysis was based on a suite of 19 bioclimatic parameters (Table 1.4) previously compiled from WorldClim climate layers (Hijmans et al. 2005; Waltari et al. 2007) at a pixel resolution of approximately 5 km^2. Model calibrations were performed using 75% of the data set as a training group and then tested using the remaining 25% (Evans et al. 2009). The program was set to remove multiple presence records from individual grid cells due to the clustering of individuals within many sampling locales. In addition, I reduced the effects of spatial autocorrelation using a split-sample approach (Fielding and Bell 1997; Parolo et al. 2008), dichotomously separating the geographically closest sample pairs into training and test groups. Initially, a full model was run and "Area Under the *R*eceiver *O*perating *C*haracteristic (*ROC*) Curve" (AUC) values for each bioclimatic parameter were acquired. To obtain a reduced model, I eliminated all parameters with an AUC below 0.75. I also verified the overall AUC for each model based on 100 bootstrap replicates in the program R 2.8.1 (The R Foundation for Statistical Computing, Vienna, Austria) by comparing between presence and background data, the latter being random points across the study area substituting for absence data. A minimal AUC of 0.75 for the test group was considered a threshold for good model performance (Elith et al. 2006; Suárez-Seoane et al. 2008). Temporal transferal modeling from the current distribution to the LGM was applied drawing from paleoclimatic information captured in the

Community Climate System Model CCSM (Otto-Bliesner et al. 2006). I created binary maps of suitable and unsuitable habitat using ArcGIS 9.2 (ESRI Corp., Redlands, CA) by averaging three independent Maxent runs. Among the thresholds tested by the program, the cutoff of suitable habitat was chosen at a fixed cumulative probability of 10, a level rejecting the lowest 10% of predicted logistic values. Although somewhat arbitrary, this level was selected based on a more conservative interpretation of habitat suitability, which still maintained a low omission rate (Pearson et al. 2007). I compared the suggested distributions of current and paleoclimatic populations with the distribution of genetic variation in the Flammulated Owl.

Results

Phylogenetic patterns among populations

From all 163 individual samples, we identified 36 segregating sites and 34 different haplotypes of which 13 (38.2%) were shared by multiple individuals and 21 (61.8%) were represented in only one individual. Three haplotypes (H2, H5, and H6) were found in at least 10% of all individuals with the most common one (H6) carried by 34.4% of all Flammulated Owls in the study and occurring in every sampling locality. The largest distance between any two haplotypes was eight mutational steps. The shallow matrix of genetic relationships was visualized in a median-joining haplotype network (Fig. 1.1). Latitudinal color coding of haplotypes within the network did not uncover a geographic pattern among the samples.

A statistical parsimony network from TCS resulted in identical topology (not shown; refer to Fig. 1.1). Nesting of clades produced twelve 1-step, five 2-step, two 3-step clades, and the entire network as 4-step clade. Among 1-step clades, one clade (1-9) had a significant departure from the null hypothesis of no geographic association (Templeton et al. 1995). Of all 2-step clades, clade 2-1 included clade 1-9 and showed significant geographic structure as well. Based on the inference key, both of these clades in question underwent restricted gene flow with IBD.

We conducted AMOVA across all sampling locations (Excoffier et al. 1992) and estimated that the greatest part of genetic variation encountered was captured within (93.8%) populations. Only a small fraction (6.2%; $p < 0.001$) accounted for variation among localities surveyed in this study. Haplotype diversity indices (h) in most population samples ranged between 0.709 and 0.894 (Table 1.1). Lower estimates came from the southern Sierra Nevada mountain range sample with 0.628 and the non-migratory population from Michoacán with 0.485. Similarly, nucleotide indices (π) were distributed from 0.00130 to 0.00309 with Michoacán as an outlier with a value of 0.00058. The population from southern Utah had the most unique haplotypes ($n = 8$) of any sample location, but Nuevo León in northeastern Mexico harbored the most private haplotypes ($n = 5$; Table 1.1) followed by southern Utah ($n = 4$) and Arizona, Idaho, and southern Oregon ($n = 3$). Only pairwise F_{ST} comparisons involving Nuevo León proved to be significant after Bonferroni correction ($\alpha = 0.0038$). This revealed a subdivision (Hartl and Clark 1997) between the birds from the Sierra Madre Oriental and the other populations (Table 1.1).

To test genetic separation of population samples from each other, we predetermined a subdivision of two groups (K) into a Samova analysis. Although not statistically significant, the result separated Nuevo León from all other population samples, which explained 21% of the total genetic variance found in all samples (F_{CT} = 0.209; p = 0.071). Increasing K to three, Arizona was selected as an additional group and the F_{CT} decreased to a significant 15.7% (p = 0.013; Table 1.2). However, 83% of genetic differences were explained by variation within populations (p < 0.0001) and a mere 1.3% was attributed to variation among populations within groups (p < 0.001).

I investigated IBD by plotting genetic [G_{ST}/(1-G_{ST})] against geographic distance between population samples (Slatkin 1993). (Fig. 1.2). Implementing all distance comparisons, a significant correlation was observed between the two distance measures (p < 0.0001; R-squared = 0.285). Therefore across all samples IBD is evident. Reducing the data set to populations from the United States and Canada only, the relationship disappears (p = 0.796; R-squared = 0.001) indicating genetic exchange uninhibited by geographic distance among the northern samples.

Gene flow, effective populations sizes, and TMRCA

The proportion of private haplotypes in populations can be informative about effective population sizes and migration rates between populations. We regressed the proportion of private haplotypes versus an independent theta *k* (Ewens 1972) and plotted a 95% C.I. estimate to locate outliers (Fig. 1.3). Confirming previous results from analyses on population structure, the population sample from Nuevo León emerged as distant outlier above the expected regression line indicating isolation from other

populations. Immigration and emigration rates were expected to be lower than among other locations. Arizona and Idaho (identical regression value) also lie slightly outside the 95% C.I. On the other end of the spectrum, the data showed increased gene flow to and from the locality in western New Mexico.

We calculated effective populations sizes and migration rates for Nuevo León and a combined northern data set (all Canadian and US populations), using the program Migrate-n (Beerli 2006). Birds from Michoacán were excluded due to their remote location and uniquely low diversity indices (Table 1.1). For the combined northern population, the sample size of eleven achieved in Nuevo León was matched for ten independent runs by selecting individuals at random. No major deviations were observed between the random sample runs. Standard errors of estimate averages stayed within 6.6% of the means, the largest variation coming from Θ of repeatedly redrawn northern samples. Calculations of Θ for both populations appeared to be similar (Fig. 1.4). Median estimates for northern birds had an average of 0.0056 (95% C.I. 0.00050 - 0.01275), closely matched by Nuevo León with 0.0051 (95% C.I. 0.00025 - 0.01250). To calculate maternal N_e, we applied a generation time of three years (Brommer et al. 2004; Woudenberg and Kirk 1999). Together with $\mu = 1.195 \times 10^{-8}$, N_e for the northern and Nuevo León populations were quantified at 157,000 and 143,000 respectively. The migration rate parameter M indicated gene flow into Nuevo León at nearly twice the rate as in the opposite direction (Fig. 1.4). Immigration into Nuevo León occurred at 1.08 female migrants per generation (N_em), a measure near the threshold of either immigration or mutation as predominant driver of variation in a population (Hartl and Clark 1997).

Lower emigration from Nuevo León into the northern localities was calculated at 0.51 female migrants per generation demonstrating a higher importance of drift in contributing genetic diversity to the population. The northern region was more likely to be the origin of the most recent common ancestor among all samples (64.3%; $\sigma = 2.8\%$), with a TMRCA of approximately 98,000 years (95% C.I. 38,228 - 157,624). Rates of gene flow based on F_{ST} (Hudson et al. 1992b) and relative population sizes (Nei 1982) indicated higher rates of gene flow (N_em) among localities outside of Nuevo León (F_{ST}-based; 11.08 - 116.77 | based on relative population size; 5.78 - 12.93) compared to gene flow between Nuevo León and all others (F_{ST}; 1.81 | rel. pop. size; 2.47).

Demographic history

We plotted observed mismatch distributions against estimated curves for a model of recent population expansions (select samples in Fig. 1.5). All but two population samples (western and southern New Mexico) did not differ significantly from a suggested model of recent population expansion. Four populations, British Columbia, Nuevo León, northeastern Oregon, and northern Utah visually revealed some departure from a unimodal pattern without violating the sum of square test statistic of deviation from expectation. Nuevo León and eastern Nevada showed significantly high *R* values of ragged distribution curves, an indicator for a stable population from demographic perspective (Table 1.3).

Neutrality indices such as Tajima's *D* and Fu's F_s may provide information on recent changes in demographic histories as well, given the assumption of neutral evolution of the applied markers (Fu 1997). Contrasting the results from mismatch

distributions, only the population sample from southern Utah (-3.580, p = 0.0067) showed a significant negative deviation from zero in its F_s estimate (-3.580, $p < 0.001$; $\alpha = 0.02$) among individual sampling regions (Table 1.3). No other significance was observed in either D or F_s except for pooled overall estimates in either parameter (D = -2.084, $p < 0.05$; F_s = -30.515, $p < 0.0001$).

We performed a Bayesian skyline analysis taking advantage of coalescent strategy to estimate demographic changes through time (Fig. 1.6). To accommodate for the high demand for informative data in the Beast analysis and justified by the limited separation among all populations (6.2%, AMOVA), Nuevo León was pooled with all other samples. Once again, we removed Michoacán from the data set based on its remote location and low genetic diversity. Applying a μ of 1.195×10^{-8}, the effective population size appeared to have moderately increased in the last 45 ky. Nonetheless, there was a large error surrounding the median estimate. After 180 million generations, we obtained ESS values for all Bayesian estimates of at least 245.44. Beast was used to calculate a median TMRCA of 131,500 years (95% C.I. 51,937 - 272,374).

Ecological niche modeling and transferal

Distribution models were developed based on 88 Flammulated Owl location records. This procedure removed multiple counts in individual grid cells eliminating pseudo-replication. The number of records was reduced by Maxent from an original tally of 195, a value composed of the 163 original samples and additional territorial responses from individuals not captured. The test group for the investigation of performance for the selected reduced model consisted of 21 individuals and delivered an AUC value of 0.983

with a standard deviation (σ) of 0.003 (Fig. 1.7). Maxent was used to estimate a variety of logistic threshold values with corresponding omission rates and fractional predicted areas. At the fixed cumulative threshold of 10 and a logistic value of 0.1361, populations found at the present time in the Rocky Mountains, the Intermountain West, and central-southern British Columbia were not represented on the map during the LGM (Fig. 1.8 A). A continuous band through Arizona, the Sierra Nevada range, the southern half of the Cascade mountains, and the California coastal ranges likely maintained a climatic environment favorable for this owl species 21 kya. Sierra Madre Occidental populations were in a connected area of suitability and birds from Nuevo León (NE Mexico) were part of a remote splinter population. The expected current distribution of suitable habitat roughly matched known range maps (McCallum 1994a) covering the entire length of the Cascade and Sierra Nevada ranges (Fig. 1.8 B). From there it spread across the sky islands of the Great Basin and Intermountain West in Nevada, Utah, and Arizona to the Rocky Mountains of New Mexico, Colorado, Montana, and Idaho. In Mexico, the model suggested a current range of two separated regions (Chihuahua and Durango) in the Sierra Madre Occidental, remote and small patches in Nuevo León and Coahuila (Sierra Madre Oriental), and a mosaic of scattered sections along the TVB into Oaxaca. On a large scale, areas where past and present occupancy generally overlapped, area coverage was more extensive and continuous during LGM conditions. According to climatic estimates, Flammulated Owls expanded in a northeastern direction from suitable habitat in the United States and experienced limited contraction throughout Mexico since the LGM.

Discussion

Population structure, resident population, and gene flow,

I encountered high levels of panmixia among most localities. All populations with the exception of Nuevo León were genetically similar and appeared to share a common recent history. Multiple analyses confirmed relatively high levels of gene flow preventing geographic structure from occurring in Canada and throughout the United States. Nonsignificant pairwise F_{ST} estimates, IBD analyses (including NCPA), and Samova analyses, all indicated strong connectivity among the localities particularly outside of Mexico. Genetically, the non-migratory southern population in Michoacán did not differ in structure from Canada and US populations either. Nevertheless, it only featured the two most common haplotypes found in the study (Fig. 1.1) resulting in the lowest genetic diversity indices across all measured localities (Table 1.1). Samova even grouped birds from Michoacán with US and Canada populations indicating a lack of genetic divergence between migratory and resident birds. Furthermore, results obtained using Migrate (Beerli and Felsenstein 2001), regression analysis of private haplotypes (Goodacre et al. 2005), and migration estimates calculated from F_{ST} (Hudson et al. 1992b; Nei 1973) confirmed high migration rates among most populations. Flammulated Owls are known for extensive site tenacity among adult breeding birds (Reynolds and Linkhart 1987), but knowledge on juvenile dispersal is lacking (McCallum 1994b). The high rate of gene flow among most populations implies dispersal by young and non-breeding adults on a large scale. Vast dispersal patterns and corresponding high levels of gene flow have been described in the Boreal Owl (*Aegolius funereus*) as well. However, long-term persistence

among low-density populations (Hayward et al. 1993) rather than density-dependent dispersal may be causing the gene flow levels observed in this sedentary Circumboreal taxon (Koopman et al. 2007).

Compared to the birds from US and Canada populations, the history for Nuevo León was unique, which is congruent with the genetic pattern observed in the MacGillivray's Warblers (Milá et al. 2000). Significant F_{ST} analyses and the high proportion of private haplotypes in Nuevo León (Fig. 1.3) suggested recent isolation and reduced migration from all other regions. Ecological niche modeling for the LGM confirmed past geographic isolation of this region (Fig. 1.8). Unlike the high female migration rates observed among US and Canada populations, rates between Nuevo León and its northern equivalents were small and asymmetrical. Immigration to Nuevo León was measured near the equilibrium of 1 where neither gene flow nor genetic drift acts as predominant factor driving allele frequencies. Gene flow leaving Nuevo León was smaller, therefore it played a minor role in the evolutionary path for the population to the north. This suggested in effect an evolutionary source (US, Canada) - sink (Nuevo León) scenario without the inherent habitat differences, which generally lead to reproductive surplus or deficit respectively (Kawecki and Holt 2002; Pulliam 1988). Furthermore, coalescent analysis in Migrate-n determined that the most recent common ancestor had a 64% chance of originating outside of Nuevo León, which corroborates historically low levels of gene flow leaving northeastern Mexico.

Demographic history

I implemented a variety of methods to test population expansion as result of retreating glaciers during the past 20 ky. My results were equivocal towards a pattern of sudden expansion throughout Canada and the United States, but do support a more moderate range shift from western refugia. Most mismatch distributions of individual populations matched the curve of all migratory birds combined (Fig. 1.5 A). Their unimodal distributions fit a model of recent and sudden expansion into the current range. Populations in New Mexico were the only cases that departed significantly from the expansion model, suggesting instead demographic stability. Across many localities in the US and Canada, genetic diversity indices were relatively high representing population stability over time (Hewitt 1996). Neutral tests of evolution (Tajima's D and Fu's F_s) did not confirm demographic expansion of the Flammulated Owl into regions mostly affected by expanding glaciers, except for the combined sample across all populations and the single group from southern Utah (Table 1.3). Although coalescent Bayesian skyline analysis testing populations sizes over time found an increasing curve across all localities, the obtained error could have allowed for a stagnation or even decrease in size as well (Fig. 1.6). However, single locus estimates of Bayesian skylines are problematic and adding additional independent markers would increase estimate accuracy and reduce errors (Heled and Drummond 2008). Significantly high raggedness values for mismatch curves in the Nuevo León population (0.307; Table 1.3) corroborate the expectation of population stability in an area with evidence of suitable habitat during the LGM (Milá et

al. 2000). Across the board, expanding populations following retreating glaciers were only found in very limited localities in the study.

Distribution of molecular diversity

Molecular diversity indices such as haplotype (*h*) and nucleotide (π) diversity can shed light on demographic history. High π represents genetic divergence within a population (Fry and Zink 1998) and is found in localities showing longterm stability, whereas *h* indicates levels of gene flow including more recent immigration (Avise 2000). Indices for most populations in this study were comparable (overall π = 0.00226, *h* = 0.841) with other genetically diverse avian taxa located in western North American mountains (Spellman and Klicka 2006). The values did exceed those of populations which have presumably undergone a sudden recent expansion (Milá et al. 2000; Milá et al. 2007). Minor deviations were detected for π among several northerly migratory populations. British Columbia birds demonstrated lower nucleotide diversity (0.00188; average π = 0.0023, S.D. 0.0005), an observation expected at the northern fringe of the species range, assuming a leading edge hypothesis (Hewitt 2000; Ibrahim et al. 1996). Furthermore, similarly low numbers were detected for samples in the two populations surveyed in Nevada (NV East = 0.00166; NV North = 0.00158). It is notable that Nevada birds were found in more remote and fragmented regions within the northern distribution (Fig. 1.8 B), where habitat fluctuations may prevent longterm establishment and stability in populations (Barrowclough et al. 2006; Bech et al. 2009). In these populations, *h* did not drop as strongly as π (average *h* = 0.807, S.D. 0.089). The pattern of increased *h* in relation to low π is frequently expressed in populations which have gone through a rapid

expansion or recolonization (Avise 2000), a likely scenario for birds in British Columbia and throughout Nevada. Relatively low degrees of both indices were discovered in birds along the Sierra Nevada (0.628 and 0.0013, h and π respectively) and particularly in the resident population of Michoacán, Mexico (0.429; 0.00058). Low values originate from either a recent founder effect after an expansion or population bottleneck (Cadahía et al. 2007; Grant and Bowen 1998). Previous phylogeographic studies on a variety of western birds have indicated a pattern of expansion into greater North America from southern refugia (Milá et al. 2006; Zink 1997). Southward expansions from northern refugia appear to be less common. Pygmy Nuthatches are believed to have expanded in multiple directions including southward towards Mexico from a refuge located in southern California (Spellman and Klicka 2006). For Flammulated Owls, genetic diversity distributions suggested a similar pattern with higher diversity to the north and subsequent expansion into the southern resident population of Michoacán. The low value from the Sierra Nevada range is surprising and challenges the validity of its habitat suitability levels during the LGM (see ENM results). In the last 60 years, Mexican forest regions have experienced deforestation rates which are among the highest in the world (Ochoa-Gaona and González-Espinosa 2000). These practices may have pushed the Michoacán population to small forest stands at higher elevations, which were too remote to harvest economically (M. Cuarao-Barajas, pers. comm.), but where genetic variation was depleted as a result.

A high proportion of private haplotypes can be explained by large historical effective populations sizes (Goodacre et al. 2005), reduced gene flow (Slatkin 1985), and

as a signal of isolation (Helgason et al. 2001). Populations lacking private haplotypes had generally lower diversity indices, such as Michoacán, Sierra Nevada, British Columbia and birds from Nevada. Throughout the range of migratory Flammulated Owls, eight populations marked various proportions of private haplotypes with Nuevo León retaining the highest value followed by southern Utah, Arizona, Idaho, and southern Oregon (Table 1.1). Reduced migration rates explain the observation for Nuevo León, but high a proportion of private haplotypes in other populations in combination with high genetic diversity raise serious questions about the validity of the putative distribution of Flammulated Owls as suggested by palaeoclimatic niche models in Maxent (Fig. 1.8). Localities throughout the current distribution have likely served as stable habitats beyond the last glacial maximum, but were not captured by maximum entropy analysis.

Historical reconstruction

The evolutionary history of the Flammulated Owl can be reconstructed through the Holocene and the late Pleistocene. Estimates of the TMRCA of all Flammulated Owl haplotypes were recent, either 98 ky and 132 ky (with significant error). However, substitution rate estimates are believed to be faster for very recent divergence events, consequently the use of universal rates of evolution applied to recent events should be treated with caution (Ho et al. 2005; Ho et al. 2008). As a result, the TMRCA obtained in this study was likely overestimated.

Given the understanding of population genetic responses to either population stability or isolation in glacial refugia (Spellman and Klicka 2006), the high genetic diversity indices, large proportions of private haplotypes, and the departure from an

expansion model along many localities were unexpected in the temperate region of North America. Two possible scenarios could explain this pattern in the Flammulated Owl. First, the LGM distribution suggested by ENMs along southwestern mountain ranges may not have captured the true extent of the historic presence of the species. Shortcomings of Maxent have recently been described on the basis of geographic distribution simulations (Godsoe 2010) and could have led to the omission of locations with high genetic diversity (Idaho and Oregon NE), large proportions of private haplotypes (Idaho and Utah S), or bi-modal mismatch distributions (New Mexico). Multiple refugia of mixed conifer and aspen across the northern and southern Rocky Mountains during the LGM (Li 1986; Yansa and Ashworth 2005) could have maintained population stability over time for the Flammulated Owl. Second, Flammulated Owls have likely tracked their optimal climatic envelope throughout the last glacial cycle of the Pleistocene (Fig. 1.8 A), accumulating high genetic diversity in multiple refugial populations along western mountain ranges and distribution of this diversity throughout recently colonized areas because of panmictic dispersal behavior. A similar accumulation of genetic diversity was previously described in the Song Sparrow (*Melospiza melodia*) by Fry and Zink (1998). However, the genetic diversity indices clearly suggested historical stability in many sampled localities for the species, disproving a recent expansion or colonization except for populations in the sky islands of Nevada and at the northern edge in British Columbia. The population history of the Flammulated Owl is comprised of a combination of characteristics observed in other North American avian taxa. It includes the possibility of a southerly range shift from suitable habitat after the

LGM (Spellman and Klicka 2006), the early stages of isolation observed in the population from Nuevo León (Milá et al. 2000), and populations stability throughout much of the North American distribution. However, we may be able to evaluate the distribution of genetic diversity more precisely using a more fine-scaled approach involving landscape and ecological factors including patch connectivity, patch sizes, or habitat quality may shed some light on the distribution and history of the species.

Table 1.1: Diversity statistics for regional population localities including sample size (N), number of all (Hap) and private haplotypes (Priv), proportion of private haplotypes (% Priv), haplotype diversity (Hd), nucleotide diversity (π) significant pairwise F_{ST} values among major sampling regions after Bonferroni correction. Comparisons of all regions to Nuevo León (NL), Mexico, provided the only significant values.

Location	**N**	**Hap**	**Priv**	**% Priv**	***h***	**π**	**F_{ST} vs Nuevo León**	
Arizona	10	6	3	0.5	0.889	0.00220	0.160	*
Brit. Columbia	10	4	0	0	0.778	0.00188	0.254	***
Idaho	10	6	3	0.5	0.889	0.00309	0.219	**
Michoacán	12	2	0	0	0.485	0.00058	0.216	*
New Mexico W	14	7	0	0	0.758	0.00247	0.220	***
New Mexico S	12	7	2	0.286	0.879	0.00241	0.173	**
Nevada E	14	5	0	0	0.802	0.00166	0.230	***
Nevada N	11	5	0	0	0.709	0.00158	0.272	**
Nuevo León	11	6	5	0.833	0.727	0.00237	N/A	
Oregon NE	10	5	1	0.2	0.756	0.00300	0.237	***
Oregon S	12	7	3	0.429	0.894	0.00260	0.182	**
Sierra Nevada	13	5	0	0	0.628	0.00130	0.300	***
Utah N	12	7	2	0.286	0.894	0.00245	0.251	***
Utah S	12	8	4	0.5	0.894	0.00270	0.173	**
Overall	*163*	*34*			*0.841*	*0.00226*		

* $p < 0.01$, ** $p < 0.001$, *** $p < 0.0001$

Table 1.2: AMOVA analysis under Samova design with predetermined group number (K) of three, of Nuevo León, Arizona, and all remaining population samples combined. A geographic framework using location data was implemented in the method.

Source of variation	***d.f.***	**Sum of squares**	**Variance components**		**% of variation**
Among groups	2	8.442	0.16764	Va	15.70
Among populations within groups	11	11.649	0.01468	Vb	1.37
Within populations	149	131.939	0.88550	Vc	82.93
Total	162	152.031	1.06782		
Significance tests	p				
Vc and F_{ST}:	0.00000				
Vb and F_{SC}:	0.00098				
Va and F_{CT}:	0.01271				

Table 1.3: Estimates of selective neutrality (*D* and F_s) and raggedness (*R*) of mismatch distributions. Significantly negative values in neutral markers for *D* and F_s indicate deviation from neutral evolution or recent population expansion. Significance level for Fu's F_s is at $\alpha = 0.02$ (Fu 1997). Large significant *R* values represent more ragged mismatch distribution curves of predominantly stationary populations.

Location	**N**	**Tajima's *D***	**Fu's F_s ($\alpha = 0.02$)**	**Raggedness index *R***
Arizona	10	-1.116	-2.082	0.079
British Columbia	10	0.385	0.048	0.153
Idaho	10	-0.861	-1.207	0.075
Michoacán	12	1.066	1.003	0.236
New Mexico W	14	-1.612	-2.006	0.035
New Mexico S	12	-0.537	-2.557	0.189
Nevada E	14	0.303	-0.844	0.174 **
Nevada N	11	-0.152	-1.396	0.030
Nuevo León	11	-1.163	-1.607	0.307 **
Oregon NE	10	-0.517	-0.105	0.129
Oregon S	12	-1.129	-2.330	0.080
Sierra Nevada	13	-1.182	-1.570	0.048
Utah N	12	-0.486	-2.510	0.074
Utah S	12	-1.005	-3.580 *	0.074
Overall	163	-2.084 *	-30.515 **	0.052

Tajima's *D* and *R*: * $p < 0.05$, ** $p < 0.0001$
Fu's F_s: * $p < 0.02$, ** $p < 0.0001$

Table 1.4: Bioclimatic variables used in the ecological niche modeling software package Maxent. The data were compiled from WorldClim version 1.4 and implemented into Maxent. Asterisks indicate variables removed for the reduced model.

Bioclimatic variables	Description
BIO1	Annual mean temperature
BIO2*	Mean diurnal temperature range
BIO3*	Isothermality (mean diurnal range/temperature annual range)
BIO4	Temperature seasonality
BIO5	Maximum temperature of warmest month
BIO6	Minimum temperature of coldest month
BIO7	Temperature annual range
BIO8	Mean temperature of wettest quarter
BIO9	Mean temperature of driest quarter
BIO10	Mean temperature of warmest quarter
BIO11	Mean temperature of coldest quarter
BIO12*	Annual precipitation
BIO13*	Precipitation of wettest month
BIO14*	Precipitation of driest month
BIO15*	Precipitation seasonality
BIO16*	Precipitation of wettest quarter
BIO17	Precipitation of driest quarter
BIO18*	Precipitation of warmest quarter
BIO19	Precipitation of coldest quarter

Table 1.5: Summary of Maxent results at common threshold levels averaged over three runs. Thresholds are listed in ascending order of logistic value. Larger values are more restrictive in predicting suitable habitat (see fractional predicted area), but will have an increased rate of omitting presence data points. The minimum training presence (italic) provided the largest logistic threshold level without omitting any implemented data locations. The fixed cumulative value 10.0 threshold (bold/italic) was chosen to reduce overestimation while still maintaining a low omission rate.

Threshold descriptions	**Logistic threshold**	**Fractional predicted area**	**Omission rate**
Fixed cumulative value 1.0	0.0110	0.2235	0.0000
Balance training omission, predicted area and threshold value	0.0304	0.1599	0.0000
Fixed cumulative value 5.0	0.0641	0.1190	0.0000
Minimum training presence	*0.0996*	*0.0982*	*0.0000*
Fixed cumulative value 10.0	***0.1361***	***0.0824***	***0.0152***
Equate entropy of thresholded and non-thresholded distributions	0.1469	0.0784	0.0152
Maximum training sensitivity plus specificity	0.2625	0.0500	0.0202
Equal training sensitivity and specificity	0.3082	0.0419	0.0455
10 percentile training presence	0.3858	0.0311	0.0909

Figure 1.1: Median-joining haplotype network with geographic color coding along north-south axis: White - British Columbia, northeastern Oregon, Idaho, Yellow - southern Oregon, Sierra Nevada, Nevada, Utah, Green - Arizona, New Mexico, Blue-green - Sierra Madre Oriental, Black - Michoacán. Haplotype frequency corresponds with size of circles. For simplicity, the network displays the only two nested clades (1-9 and 2-1) recovered from NCPA with significant departure from null hypothesis of no geographic association. Smallest dots and hash marks represent unsampled haplotypes.

Figure 1.2: Semi-log regression plot of genetic distance over geographic distance (Slatkin 1993). Comparisons drawn in solid circles represent distances among populations within the United States/Canada. Open circles represent distance comparisons between Mexican and all other population samples. The gray dashed slope represents expected values among all comparisons (solid and open circles; $p < 0.0001$; R-squared = 0.285), the black slope illustrates Canadian and US samples only ($p = 0.796$; R-squared = 0.001).

Figure 1.3: Regression curve and 95% C.I. contrasting proportion of private haplotypes and Θ_k. Strong outliers denote increased isolation and reduced migration rates (above regression line) or clustering and increased migration (below).

Figure 1.4: Frequency plots of effective population size Θ and migration rate M parameters for all Canada and the United States populations combined in comparison to

Nuevo León. Breaks in color shading delimits 50% (black-dark gray) and 95% (dark gray-light gray) confidence intervals.

Figure 1.5: Select mismatch distributions for a pooled group (all populations included; A), northern Utah (B), southern New Mexico (D), and Nuevo León (D). Bars show observed pairwise sequence differences in a population. The line reflects an expected distribution under a recent population expansion model. Mismatch distributions for all populations not shown indicated recent population expansion (see A & B). Both populations from New Mexico differed significantly from expansion (C). Raggedness level in Nuevo León sample (D) indicated a stable population (see Table 2.5).

Figure 1.6: Bayesian skyline plot tracking changes in median effective population size through the recent history of the Flammulated Owl. C.I. of 95% was drawn inside dashed lines surrounding median estimates.

Figure 1.7: Extrinsic receiver operating characteristic (ROC) curves from test (light gray), training (black dashed), and random (dark gray) model predictions and affiliated AUC values. The result indicated model fit and range specificity of the tested taxon under the 12 variables of the climatic regime. The standard deviation was based on 500 iterations.

Figure 1.8: Estimates of suitable habitat for the Flammulated Owl predicted from transferral of ecological niche model under palaeoclimatic conditions 21 kya (A). The niche modeling output for the current bioclimatic variables as predicted by Maxent is shown on map B. The threshold for the cutoff of suitable habitat was chosen at the minimum training presence with the highest possible logistic value (0.116) without omitting any presence records.

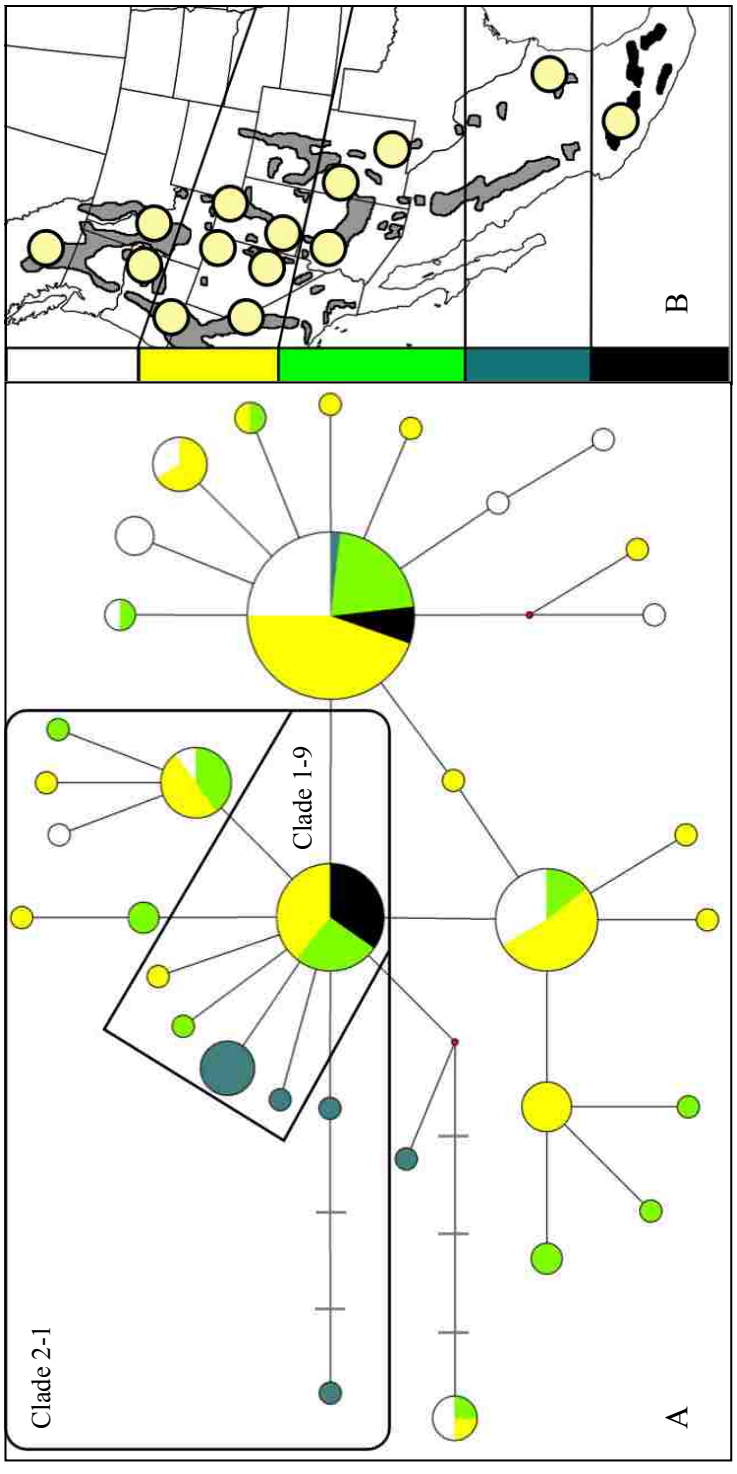

Figure 1.1

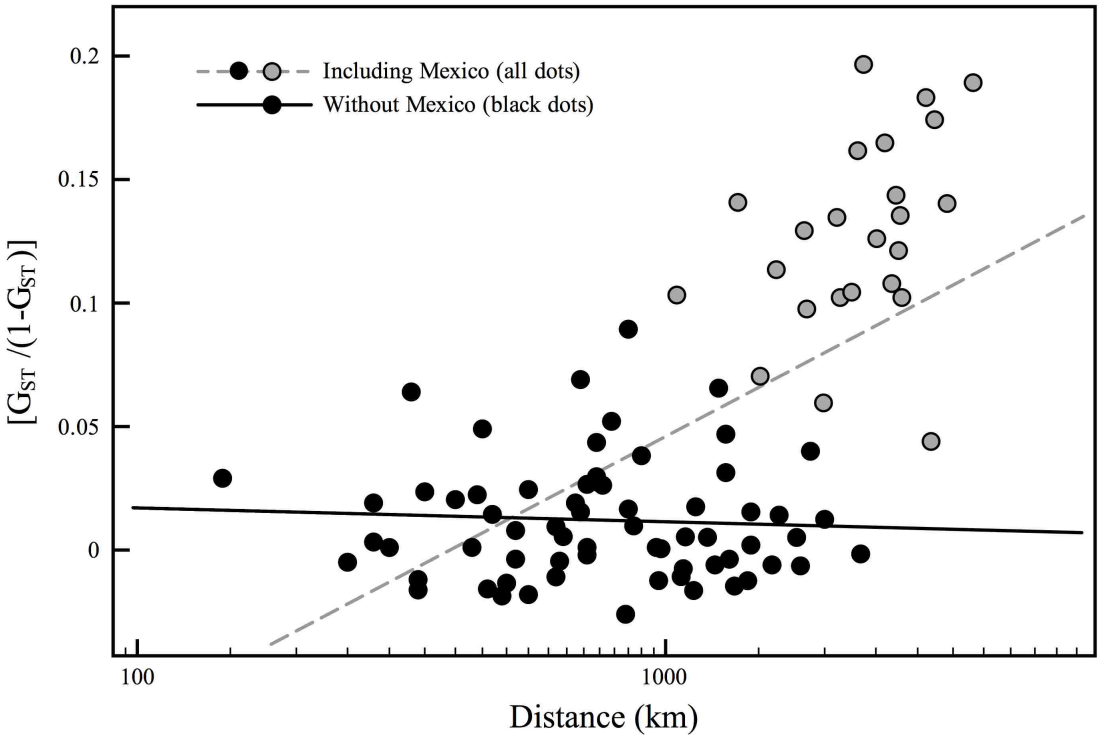
Including Mexico (all dots)
Without Mexico (black dots)
0.2
0.15
0.1
0.05
0
[G_ST /(1-G_ST)]
100
1000
Distance (km)

Figure 1.2

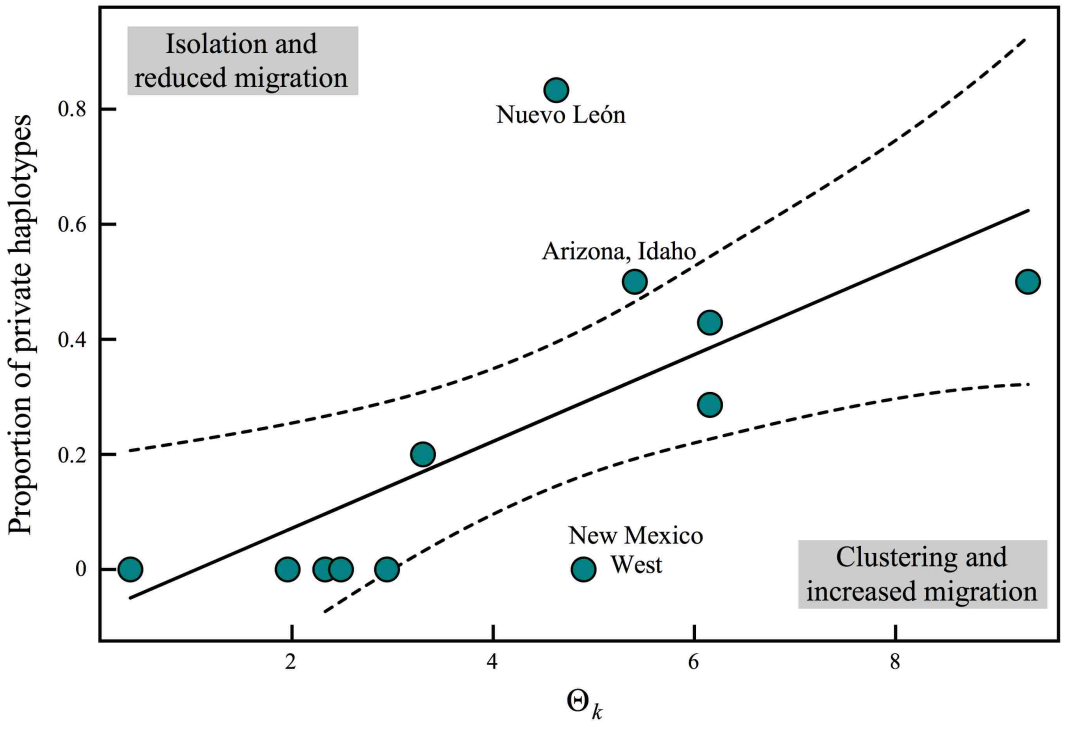
Isolation and
reduced migration
Nuevo León
Arizona, Idaho
New Mexico
West
Clustering and
increased migration
Proportion of private haplotypes
0.8
0.6
0.4
0.2
0
2
4
6
8
Θ_k

Figure 1.3

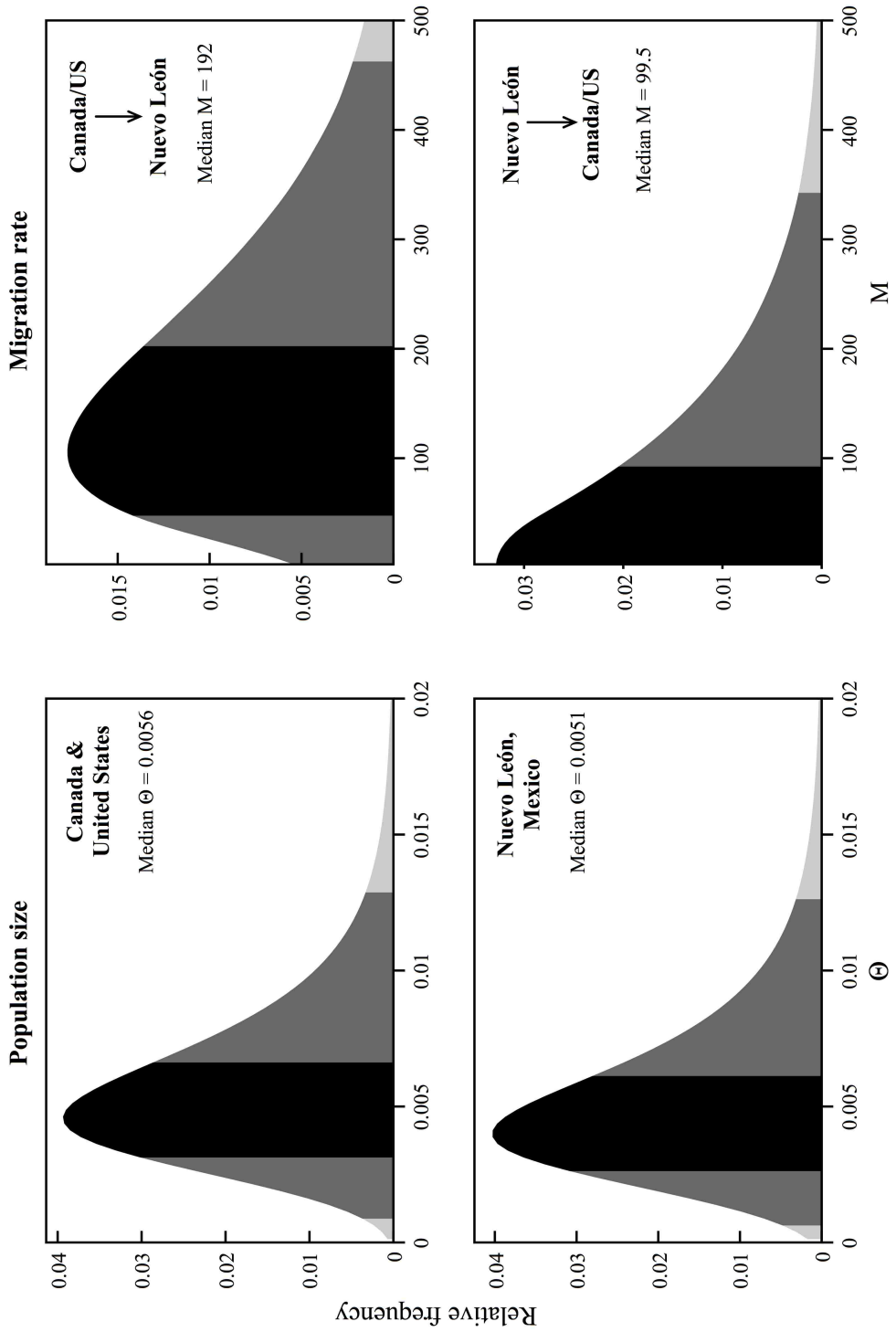
Population size
Migration rate
Canada &
United States
Median Θ = 0.0056
Nuevo León,
Mexico
Median Θ = 0.0051
Canada/US
Nuevo León
Median M = 192
Nuevo León
Canada/US
Median M = 99.5
Relative frequency
Θ
M
0
0.005
0.01
0.015
0.02
0.04
0.03
0.02
0.01
0
100
200
300
400
500
0.015
0.01
0.005
0.03
0.02
0.01

Figure 1.4

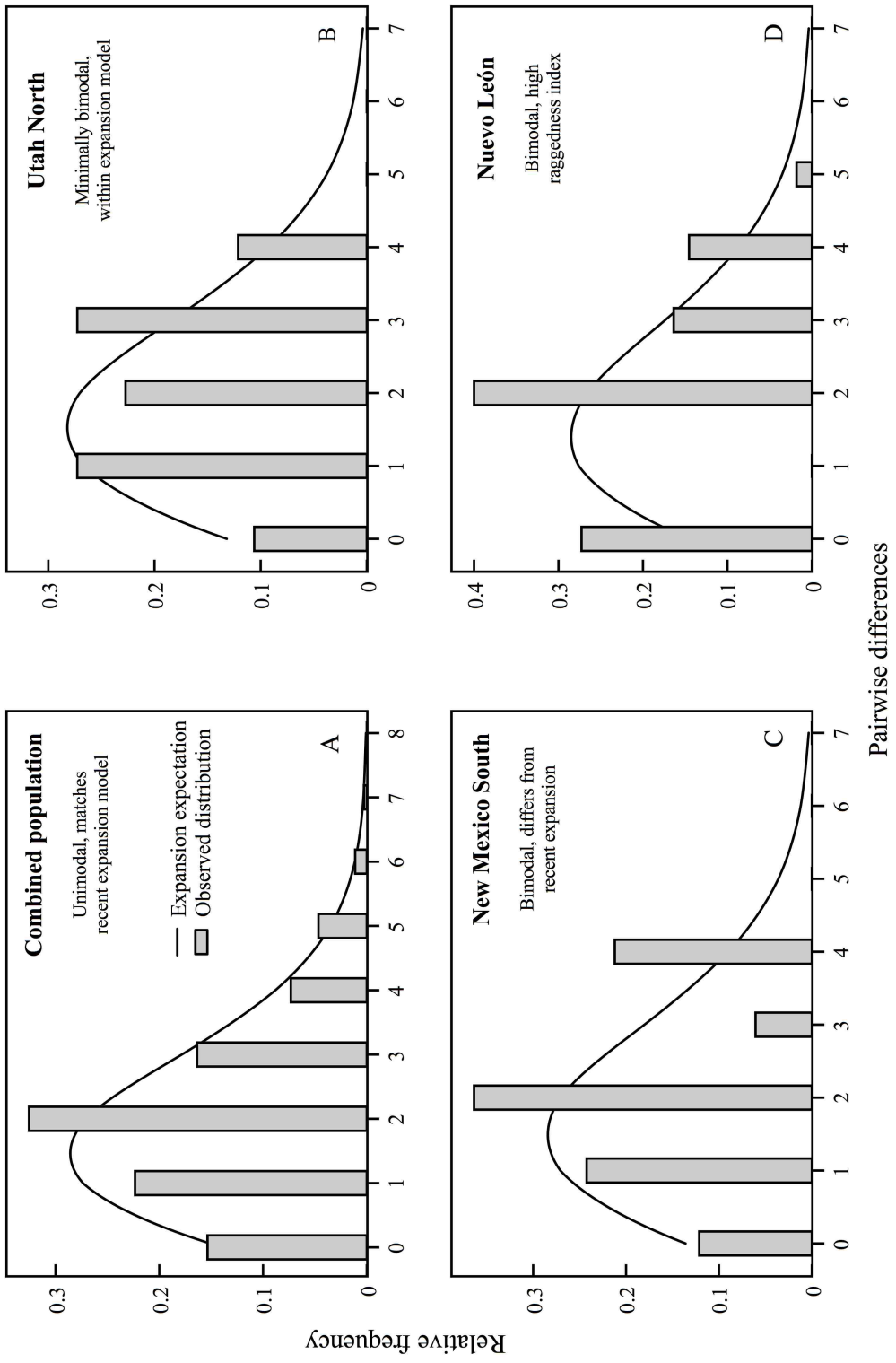
Combined population
Unimodal, matches recent expansion model
Expansion expectation
Observed distribution
A
Utah North
Minimally bimodal, within expansion model
B
New Mexico South
Bimodal, differs from recent expansion
C
Nuevo León
Bimodal, high raggedness index
D
Relative frequency
Pairwise differences

Figure 1.5

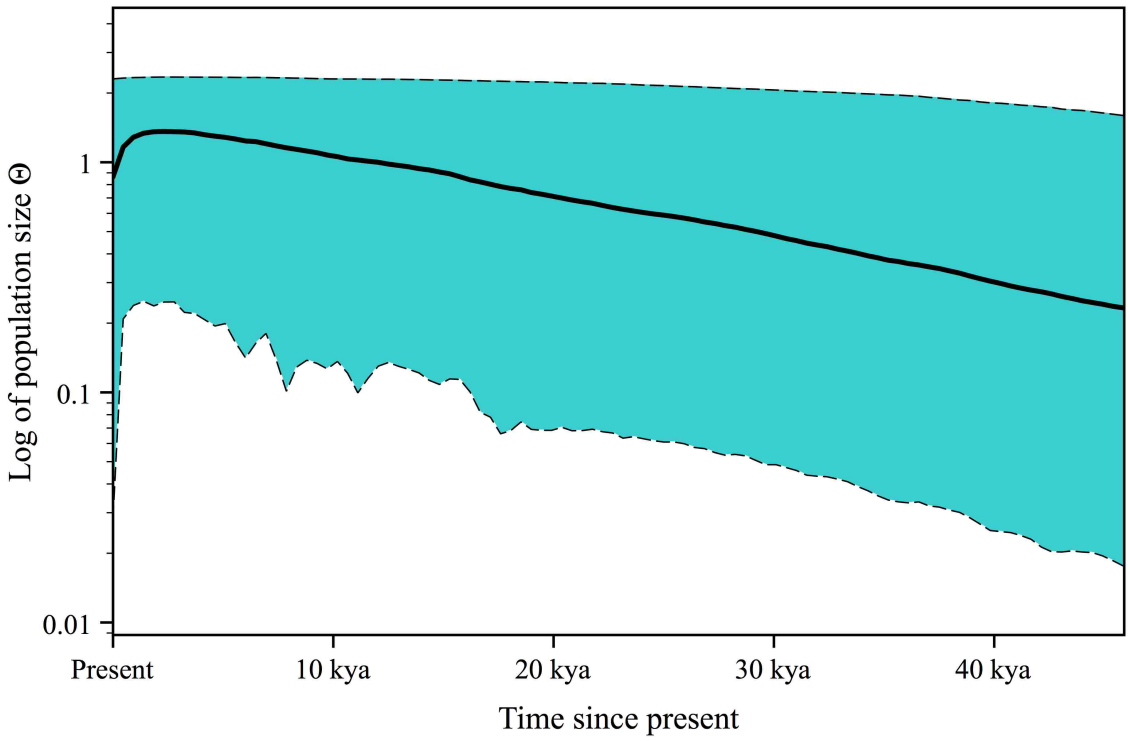
Log of population size Θ
1
0.1
0.01
Present
10 kya
20 kya
30 kya
40 kya
Time since present

Figure 1.6

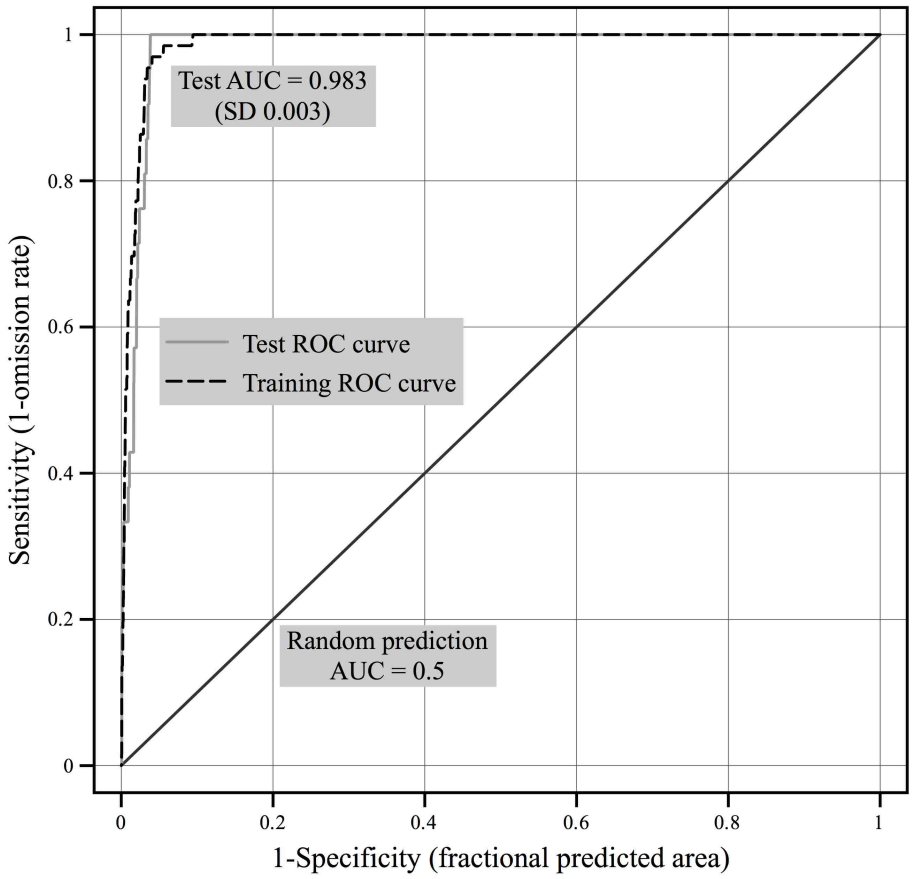
Test AUC = 0.983
(SD 0.003)
Test ROC curve
Training ROC curve
Random prediction
AUC = 0.5
Sensitivity (1-omission rate)
1-Specificity (fractional predicted area)
0
0.2
0.4
0.6
0.8
1

Figure 1.7

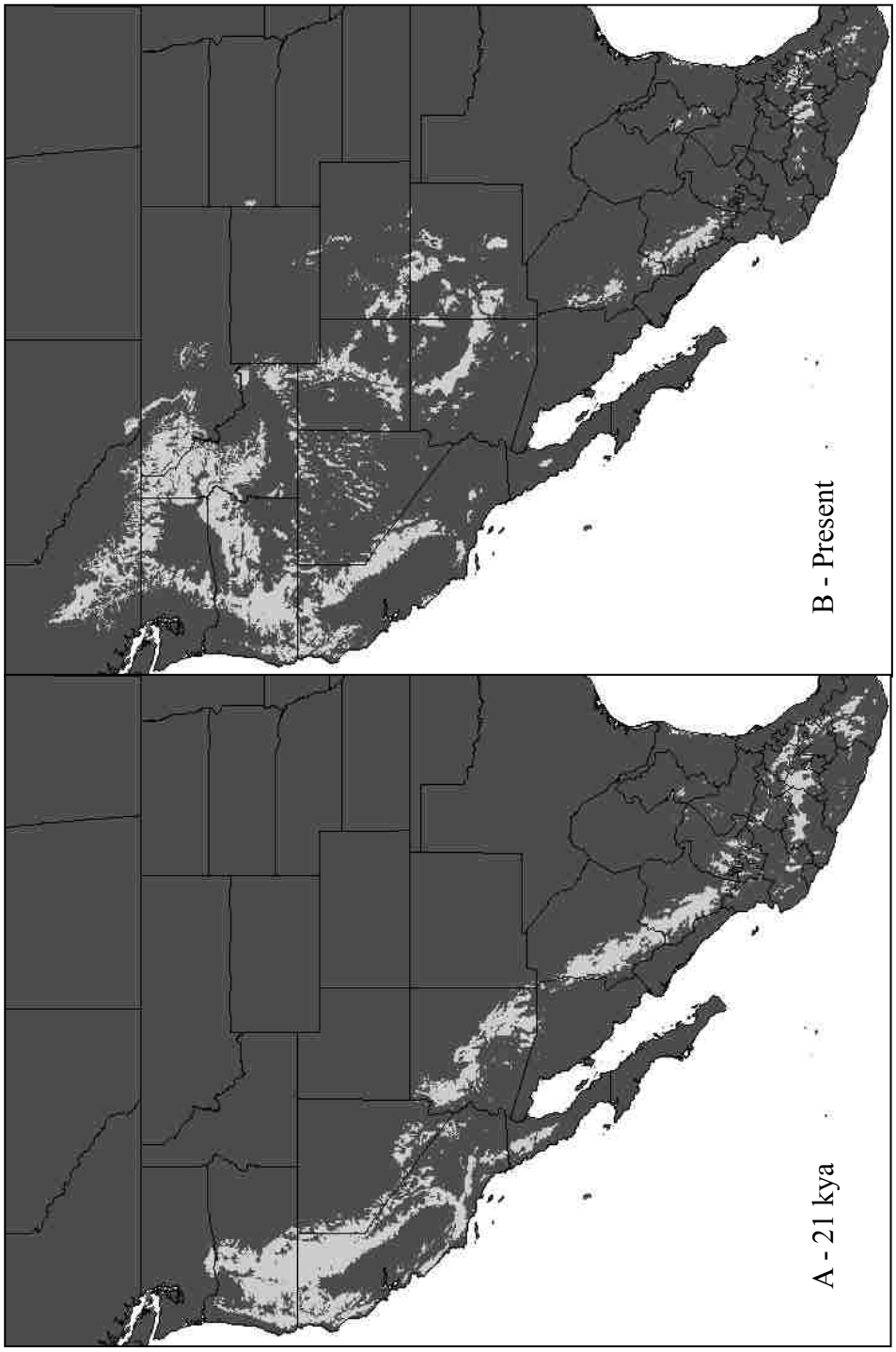

Figure 1.8

CHAPTER 2

LANDSCAPE-MEDIATED DISTRIBUTION OF GENETIC VARIATION IN THE FLAMMULATED OWL (*OTUS FLAMMEOLUS*)

Abstract

Phylogeographic approaches do not always capture the appropriate scale to clarify intraspecific population demographics and history. For the Flammulated Owl (*Otus flammeolus*), phylogeographic explanations did not capture the detail of the distribution of genetic diversity across the range. Here, I applied linear regression models to investigate relationships between landscape and ecological features with genetic diversity indices from mitochondrial ATPase sequences. The species is semi-colonial, feeds on insects, and is distributed throughout fragmented montane dry forests in southern and western North America. Population sizes, territory density estimates obtained in the field, and habitat suitability averages calculated from ecological niche modeling distributions were good predictors of nucleotide diversity. Despite the fact that the connectivity measures of isolation and proximity were not correlated with genetic diversity, proximity did show a very strong positive relationship with current population sizes in the absence of genetic variables. In the same model, habitat suitability was also strongly affiliated with population size. The results indicated that metapopulation dynamics among habitat patches of various sizes, habitat quality, and population densities are important in shaping genetic diversity and distributions in this species.

Introduction

The distribution of species across landscapes and the factors influencing intra- and interspecific diversity have been at the center of research in evolution and ecology for several decades. The groundbreaking principle of island biogeography (MacArthur and Wilson 1967) and the study of metapopulation dynamics (Hanski 2004; Levins 1969) have triggered vigorous debate following their initial exploration, but have proven to be lasting paradigms with far reaching influence on new and old disciplines alike (Lomolino and Brown 2009).

Most organisms are scattered across structured landscapes among patches of variable sizes, connectivity, and quality, which in turn impact extinction and colonization dynamics (Franzén and Nilsson 2010; Simberloff and Wilson 1969). Patch sizes and degree of isolation influence genetic drift, gene flow, and natural selection, the factors in charge of genetic variation in populations (Frankham 1996). Isolated and small populations are particularly vulnerable to extinctions caused by fluctuations and stochastic changes in the environment since they are genetically less variable due to genetic drift or reduced immigration (Ditto and Frey 2007). Whereas, high genetic diversity has been linked to increased dispersal and population sizes, low diversity can lead to a decrease in life expectancy and fitness (Vandewoestijne et al. 2008). Genetically impoverished populations often suffer from lower immune responses to disease and high parasite loads (Whiteman et al. 2006), putting a strain on fecundity (Ortego et al. 2007). Life history factors may also play a part in the success or failure of local populations. Species living in colonies or those exhibiting resource competition behavior are more

likely to face local extinction than solitary taxa or organisms “scrambling” for resources (Best et al. 2007; Lees and Peres 2008).

Within the realm of conservation biology, anthropogenically transformed landscapes have provided the most immediate testing grounds for the concepts of island biogeography and metapopulation dynamics (Hanski 2004). The genetic effects of dramatic patch size reduction and isolation due to habitat loss for species of conservation concern have received considerable attention (Gebremedhin et al. 2009; Simberloff and Abele 1976; Toro and Caballero 2005). Nevertheless, shifts in natural habitats and landscapes during the late Quaternary have also contributed extensively to the current distribution of biological diversity (Avise and Walker 1998; Smith et al. 2009) and may reflect classic metapopulation dynamics even in common taxa (O'Keefe et al. 2009). Increased rates of immigration have shown to be effective in accumulating genetic diversity, even in recently founded populations (Hansson et al. 2000) and historic bottlenecks or local extinctions have been common in many temperate taxa (Ruedi and Castella 2003; Taylor et al. 2007). Both patterns represent longterm metapopulation dynamics of recolonization and local extinction across past species distributions. However, empirical data on metapopulation dynamics of mobile species with shallow genetic structure among populations are still rare (Ortego et al. 2008; Seppa and Laurila 1999)

Ecological factors have been considered in determining species abundance at current temporal scales (Wilson et al. 2009), and also in the distribution of genetic variation across stable ecological landscapes (Muñoz-Fuentes et al. 2009; Pease et al.

2009). This diversification may not always lead to ecological speciation as observed in the classic example of cichlid fish in Eastern Africa (Schluter 1993; Wagner and McCune 2009), but landscape and ecology play an important role in maintaining variation among populations (Antolin et al. 2006). Methods in ecological niche modeling (ENM) are advancing quickly and provide a simple technique to estimate habitat affinities across entire distributions (Peterson 2001; Phillips et al. 2006). They can also be used to shed light on past distributions of species by model transferals using known palaeoclimatic variables (Peterson et al. 2007). Estimates provided by ENMs are independent measures of habitat suitability, which lend themselves for comparison with more traditional benchmarks of habitat affinities including population sizes and densities (Sattler et al. 2007) or phylogeographic patterns and genetic diversity (Cordellier and Pfenninger 2009). Unfortunately, empirical data on statistical comparisons with ecological population parameters are scarce (Strubbe and Matthysen 2009).

To avoid the limitations of low sample sizes in rare or threatened species, choosing a common taxon across various patch sizes and degrees of connectivity would certainly promote the study of metapopulation dynamics in natural populations (Ortego et al. 2008). Although illusive, the insectivorous Flammulated Owl (*Otus flammeolus*) is a common species that is found in semi-colonial clusters throughout dry and open forests in the mountains of western and southern North America (McCallum 1994a; Oleyar et al. 2003). Breeding populations not only persist in large and connected forests of the Rocky Mountains, Sierra Nevada, and Cascade ranges, but also in small stands located on sky islands across the North American west (Dunham et al. 1996; Spellman et al. 2007). The

species lacks phylogenetic structure and with the exception of one population in northeastern Mexico, gene flow among most populations across the range is very high. Genetic variation among population samples from numerous, widely scattered localities was ambiguous with regards to proposed Pleistocene refugia (Mika and Klicka, submitted). The objective of this study was to investigate which ecological and landscape factors were responsible for the geographic distribution of population sizes and genetic variation across the distribution of the Flammulated Owl. This was accomplished by testing whether either dependent variable was correlated with patch size, population territory density, isolation, proximity, and latitude. Furthermore, I investigated whether ecological niche models were good predictors for the current occupancy and genetic variation measured in the species. To meet the objectives, I used owl density estimates obtained for twelve localities during field explorations and metapopulation metrics calculated from digital distribution maps. Genetic diversity estimates were calculated for all breeding populations using 829 base pairs of the mitochondrial (mtDNA) marker ATPase 8 & 6.

Materials and Methods

Sample summary

I compiled genetic samples from 137 individuals representing 12 populations taken from throughout the species distribution (see Appendix I; samples without asterisks). The reduced sample size in comparison to . These included migratory populations from the northern extent of the range and permanent residents from southern

Mexico. For each genetic population sample, I considered local territory densities (DAREADJ), patch sizes (SIZE), a proximity metric (PROX), patch isolation (ISO), latitude (LAT), a measure of ecological population size (comprised of territory density multiplied by patch size [POPSIZE]), and a current habitat suitability estimate (MAXNOW) based on maximum entropy logistic values from ecological niche models.

Field methods

Owls were censused using recorded call playback. To increase survey efficiency at night, transects were pre-surveyed during daylight hours. I waited at the first survey point until dark before starting initial playback broadcast. Appropriate darkness was determined as the time when tree vegetation became only visible as a black outline contrasting with the sky. Before the first playback bout, I listened for up to three minutes to detect unsolicited calling by males. Then, a minute of continuous male playback was broadcast at a moderate volume imitating the male territorial call using an mp3-player connected to a self-amplified speaker. Playback was broadcast in all directions by slowly turning the speaker 360 degrees. It was followed by one minute of silence to listen for responses. I then repeated this sequence at least three times, in some cases increasing the number of sequences due to high ambient noise from wind, water, or airplanes. Initial owl responses were identified and bearings in the direction of the call response and their estimated distances were recorded. Along a transect, distances between calling stations were kept at approximately 400 meters, adjusting them to topography, vegetation, and increased ambient noise. Each response by a male bird was assumed to represent a breeding territory.

Due to the migratory nature of *O. flammeolus*, genetic samples of 137 individuals were obtained only during the breeding season. I captured most individuals using a male territorial playback call and a single mist net at locations deemed suitable during preliminary daytime surveys. Before final release, each bird was processed at the location of capture and one inner secondary flight feather and one central tail feather were saved as genetic samples.

Analytical and laboratory techniques

Total genomic DNA for all specimens was extracted from feather and tissue samples using standard protocols found in the DNeasy Tissue Kit (Qiagen, Valencia CA). For all feather samples, I supplemented the initial incubation solution with 30 µl of Dithiothreitol (DTT) to dissolve the sheath of the feather calamus. I amplified and sequenced 829 base pairs of the overlapping genetic markers ATPase 8 and 6 (ATPase) from the mitochondrial genome (mtDNA) for all 163 individuals using the primers CO2GQL (5'-GGA CAA TGC TCA GAA ATC TGC GG-3') and CO3HMH (5'-CAT GGG CTG GGG TCR ACT ATG TGH-3') (Greenberg et al. 1998; Joseph et al. 2003). PCR reactions of 12.5 µl were prepared and executed under the following amplification conditions: initial 10 minute denaturation at 94ºC followed by 40 cycles of 94ºC for 30s (denaturation), 54ºC for 45s (annealing), and 72ºC for one minute (elongation). Finally, a 10 minute extension phase was followed by a 4ºC soak. Successful amplifications were purified using the Exosap-IT (USB Corporation) purification following a heating protocol of 15 minutes at 37ºC with a subsequent phase of 15 minutes at 80ºC. Sequencing reactions of 20 µl were performed using Big Dye Terminator v3.1 (Applied Biosystems)

and purified with a magnetic bead cleanup (Agencourt Biosciences). Sequences were analyzed on an ABI 3100-Avant automated sequencer (Applied Biosystems). Sequences were aligned and verified by eye using Sequencher 4.8 (Gene Codes Corporation) and checked for anomalies (pseudogenes) (Sorenson and Quinn 1998) by comparing them to homologous mtDNA sequence from the Barred Owl (*Strix varia*).

I calculated territory densities (DAREADJ) per square kilometer (km^2) by overlaying transects on digital versions of 1:24,000-scale topographic maps (USGS) or maps available within the Google Earth 5.1 software package (Google Inc.). Each transect was assumed to cover an area of up to 400 meters broadcast reach in all directions and summed up over the entire transect length. The distance was reduced under poor wind conditions and limited forest cover. The number of encountered male response calls was divided by the area surrounding each transect. Densities from multiple transects within one population were averaged. For late season surveys (July & August), I multiplied density values by 1.65 (Barnes and Belthoff 2008) to account for the decreased response probabilities of males occupying breeding territories in this species. I tested for first order serial correlation of density from a preliminary simple regression model by applying the Durbin-Watson statistic (Durbin and Watson 1971) and Breusch-Godfrey serial correlation LM test (Breusch 1979; Godfrey 1978).

To estimate patch sizes and isolation of individual populations, I used current distribution estimates obtained from ecological niche models (Guisan and Zimmermann 2000) and applied location records from our field data collection into a maximum entropy method implemented in the program Maxent 3.2.1 (Phillips et al. 2006). From a suite of

19 previously compiled climatic layers (Hijmans et al. 2005; Waltari et al. 2007) I eliminated all parameters with an "Area Under the *R*eceiver *O*perating *C*haracteristic (*ROC*) Curve" (AUC) below 0.75 (Table 1.4). I created binary maps of suitable and unsuitable habitat using ArcGIS 9.2 (ESRI Corp., Redlands, CA) by averaging three independent Maxent runs. Among the thresholds tested by the program, the cutoff for suitable habitat was chosen at a level rejecting the lowest 25% of predicted logistic values. In doing so, I obtained maps containing all individual genetic samples within suitable habitat with the least amount of overestimation. I transferred suitability maps to the software package ImageJ 1.42q (National Institute of Health, Washington DC) for pixel calibration and patch size estimation. The sizes of disjunct patches found within one population sample were averaged. I calculated the independent variable MAXNOW from the average logistic value obtained from current niche modeling estimates using maximum entropy. Isolation estimates (ISO) were measured as total area (km^2) of neighboring patches within a buffer of 500 km in diameter (Fig. 2.1). This method has proven to be a successful predictor for animal immigration across various taxa (Bender et al. 2003). The buffer represented an assumed 1-step dispersal distance. For each population patch *i*, a proximity metric (PROX) was calculated using equation (1), where a_{ijs} is the area of neighboring patch *j* and d_{ijs} is the distance between the nearest edges of the focal patch *i* and neighboring patch *j*. Values for each neighboring patch within the buffer distance (see ISO) were summed to produce a proximity estimate for each focal patch (Wilson et al. 2009).

$$PROX = \sum_{i=1}^{n} \frac{a_{ijs}}{d_{ijs}} \quad (1)$$

Multiple linear regression (R version 2.10.1; R-Project for Statistical Computing) was used to test the effects of independent variables on the responses of nucleotide (π) and haplotype diversity (h) in our mtDNA marker ATPase 8 & 6. I used the Anderson-Darling test for normality on each variable (Anderson and Darling 1954) and applied a log-normal (ln) transformation to treat non-normal distributions of variables. A full model including the independent variables DAREADJ, POPSIZE, PROX, ISO, LAT, and MAXNOW was utilized as starting point for model selection. I used Mallows C_p statistics and plots (Mallows 1973) and the adjusted R-squared (Zhu et al. 2009) to select the best model. Mallows C_p represents a measure of model suitability for a prediction based on sum of squared errors (Ronchetti and Staudte 1994). The model with the lowest C_p-value or the highest adjusted R-squared value respectively was chosen as most adequate for our data. Variance inflation factors (VIF) were evaluated for all models (Stine 1995) and collinearity was rejected below the conservative cutoff values of five (Craney and Surles 2002). Furthermore, I separated the components (DAREADJ and SIZE) of the integrated variable POPSIZE to detect collinearity and independent effects in the model. This was accomplished by plotting residuals from the integrated simple regression (π = dependent variable, POPSIZE = independent variable) over separated observed DAREADJ and SIZE values. To test for constant variance, a studentized version of the Breusch-Pagan test for heteroscedasticity (non-constant variance) was applied to the models (Breusch and Pagan 1979; Koenker 1981).

Results

Nucleotide diversity indices (π) ranged from 0.0013 to 0.0031 with Michoacán as an outlier with a value of 0.0006 (Table 2.1). Haplotype indices (h) in most population samples ranged between 0.709 and 0.894. Lower estimates came from the southern Sierra Nevada mountain range sample with 0.628 and the non-migratory population from Michoacán with 0.485. Seasonally adjusted territory density estimates (DAREADJ) throughout the 12 localities ranged from 9.63 to 2.39 per km^2. The three highest values were encountered in Nuevo León (9.63), Idaho (9.54), and northeastern Oregon (8.21). The transects with the lowest densities were located in the Sierra Nevada (2.39) and Michoacán (3.09). The proximity (PROX) and isolation metrics (ISO; high value represents little isolation) appeared to be very high for the population in Idaho (9573.8; 49159 respectively) and low for Nuevo León, Michoacán, Nevada, and the population in Arizona (14-82.3; 1142-6976). Ecological population sizes (POPSIZE) were particularly large throughout Oregon and Idaho (316471-144790) and comparatively modest in Nuevo León, Michoacán, and Nevada (9355-558). Habitat suitability (MAXNOW) was highest in eastern Oregon, southern New Mexico, Arizona, and southern Oregon (0.797-0.739) and lowest in Michoacán and eastern Nevada (0.336-0.323). The variables SIZE, PROX, and POPSIZE required a log-normal transformation due to the lack of normality. Density estimates contained in DAREADJ were not serially autocorrelated (DW test = 2.58, $p = 0.858$; LM test = 2.068, $p = 0.15$).

I excluded genetic variation indices for the evaluation of the factors predicting population size and detected a strong correlation with the habitat suitability values

provided by ecological niche modeling (MAXNOW; Fig. 2.2). In the presence of proximity and density variables, habitat suitability exhibited strong predictive power for population sizes (Adj. $R^2 = 0.944$; $p < 0.00001$). Proximity performed similarly well in the same model ($p < 0.0005$). Therefore, I avoided potential collinearity between population size and habitat suitability by developing separate linear regression models containing either of the two independent variables for subsequent landscape genetic analyses.

Among the two genetic diversity indices examined in the study, only nucleotide diversity (π) was significantly related with any of the suggested independent landscape and ecological factors. When I excluded habitat suitability from a model with the dependent variable π, population size and density were significant predictors of π in the best fit model (Table 2.2 A). The relationship appeared relatively strong with an adjusted R-square of 0.755. Even though density is a component of population size, a visual representation, using residual values from the simple regression (2) and plotting them separately over density and patch size (SIZE) estimates (Fig. 2.3), confirmed independent behavior between density and the integrated population size (Fig. 2.3 A, B). Low VIF estimates of 1.074 in the best fit model among both independent variables (Table 2.2) demonstrated lack of collinearity corroborating the visual evidence. Populations with lower density generally underperformed with regards to the expected π (Fig. 2.3 B; see box below residual zero). Populations with higher density outperformed model expectations (Fig. 2.3 B; see box above residual zero). In contrast, the distribution of residuals across patch size (Fig. 2.2 C) closely resembled the pattern observed in the

visualization of the regression between π and population size (Fig 2.2 A). I confirmed this observation by testing collinearity with both estimates (POPSIZE & SIZE) included in the model (VIF = 20.28). Populations underperforming genetically showed similar variation in patch size than populations with higher than expected π estimates (Fig. 2.3 C; see boxes below and above residual zero).

After replacing population size with habitat suitability in a second series of model selection, my best fit model consisted of density and suitability as significant predictors for π (Fig. 2.4) featuring an adjusted R-square of 0.753. Once again, I did not detect collinearity between explanatory variables (VIF in Table 2.2 B).

Discussion

Landscape and ecological features accurately predicted Flammulated Owl distribution and genetic variation in a metapopulation framework (Vandewoestijne et al. 2008). The major conclusions we can draw from our results were: First, population sizes appeared to be strongly correlated with a model comprised of habitat suitability under current climatic conditions, proximity estimates of focal populations to their neighboring patches, and population densities. Second, indicators such as population sizes, density estimates, and habitat suitability were good predictors of genetic diversity. Third, variables linked to degrees of connectivity were not relevant for the distribution of genetic diversity, but proximity was strongly correlated with current population sizes.

Ecological niche models have recently been criticized for their limitation of habitat prediction, particularly when the organism in question is capable of using several

habitat types that are in close regional proximity (Godsoe 2010). However, pixel-specific logistic values (MAXNOW) obtained from the maximum entropy method in Maxent (Phillips et al. 2006) appeared to be strongly correlated with assumed population sizes (Fig. 2.2). Although Flammulated Owls are found using several types of forest flora (Marti 1997), they are believed to prefer dry and open montane habitats within a specific forest physiognomy (Linkhart 1984). Climatic envelopes described the habitat requirements in Flammulated Owls precisely for the scale of this study (Fig. 2.2). However, our population size estimate was strongly driven by patch sizes (Fig. 2.3 A & C) and larger patches generally provide a buffer against forest disturbance (Honnay et al. 1999). Therefore, we expected to find higher degrees of habitat suitability in larger habitat patches. In addition, areas with optimal habitat can have high colonization rates and large population sizes despite a relatively high degree of isolation from other patches (Franzén and Nilsson 2010; Grant Hokit et al. 2010).

Population densities (DAREADJ) showed a significant positive correlation to dependent variables in all best fit models tested in this study. In Flammulated Owls, population densities have been correlated with the availability of nesting cavities (Arsenault 2007). Foraging resource quality is also important for reproductive output in this species and is believed to influence higher return rates in good quality patches (Mika 2003). Abundance in both of these resources has the potential to positively impact local densities. However, density is not always positively correlated with high quality habitat (García et al. 2007). Species living in small isolated patches with limited carrying capacities often reached high population densities even when habitats were of poor

quality (Hale and Briskie 2009). High density estimates may also reflect past levels of quality and a response lag by an organism with high site tenacity (van Horne 1983). Consequently, it has been recommended to complement density estimates with an independent measure of habitat quality before making an inference on habitat quality (Vickery et al. 1992). We accomplished this by implementing ENM values of habitat suitability, which confirmed a positive correlation of both density and habitat suitability in the models for genetic diversity and population size. Furthermore, populations with high density values outperformed a model of genetic diversity explained by population sizes (Fig 2.2 A &B), whereas low density patches generally underperformed. In a study on Tree Swallows (*Tachycineta bicolor*), increased genetic variation was found in poorer quality habitat, which produced smaller numbers of offspring (Porlier et al. 2009). The authors suggested that poor habitats were in closer proximity to migration routes and early occupants, which generally consisted of genetically more diverse groups, were compelled to establish territories quickly without regard to habitat quality. In most other cases, genetic diversity was integral in maintaining high fitness levels in large and well connected habitat patches (Vandewoestijne et al. 2008; White and Searle 2007).

Patch size (SIZE), one important factor in metapopulation dynamics for colonization rates and local extinctions (Franzén and Nilsson 2010), was a good predictor of genetic diversity in Flammulated Owls. We used the more realistic population size estimate (POPSIZE) to capture patch sizes in the analyses. In mobile taxa, the chances of prospecting birds tracking down patches may simply be higher for larger patch sizes (Bowler and Benton 2005). In contrast, the degree of proximity (PROX) did not influence

the distribution of genetic variation, but was strongly correlated with population sizes. Phylogeographic analysis of the Flammulated Owl revealed that genetic distance between populations was not correlated with geographic distance, which emphasizes that isolation has a minimal impact on genetic diversity even at a deeper evolutionary timescale (Mika and Klicka, submitted). The increased accumulation of genetic diversity in large patches compared to small ones (Gotelli 1991) may be a function of a limited number of territories at smaller patches and reduced diversity as a reflection of local census numbers. This pattern is corroborated by the fact that the independent variable POPSIZE included local demographics.

The correlation of the proximity metric with population sizes may simply be a function of large patches being much closer to neighboring patches because of their size. However, the population size estimate is a more current measure of Flammulated Owl distribution than genetic diversity, which reflects a deeper temporal scale. Proximity is therefore playing a role in the immediate demographic distribution through stepping-stone dispersal inflating population sizes in nearby localities. Inevitably, genetic patterns and isolation-by-distance resulting from proximity would be eliminated by continuously high levels of gene flow (Clegg et al. 2003). Smaller populations with lower densities appeared to contain lower levels of genetic diversity regardless of distances to neighboring patches.

Although isolation appeared less important for the distribution of intraspecific diversity, Flammulated Owls exhibited a classic pattern of metapopulation dynamics. Smaller patches may have been less stable and even absent at some point in time through

natural fluctuations, but these patches were recolonized when conditions improved (Hames et al. 2001). Large patches on the other hand faced a less drastic impact from habitat fluctuations and maintained or increased genetic diversity over longer time periods. Ecological factors and landscapes played an important role in distribution, demographics, and genetic diversity in the Flammulated Owl. Incongruent patterns obtained from previous phylogeographic analyses were explained by patch and population sizes, density estimates, and habitat quality measures.

Table 2.1: Observations and estimates of dependent and independent variables for linear regression models. DAREADJ was assessed as the number of territories per square kilometer, SIZE and ISO as square kilometers, POPSIZE as product of DAREADJ and SIZE, and MAXNOW as logistic values of habitat suitability using a maximum entropy procedure. AZ = Arizona; BC = British Columbia; ID = Idaho; MX-S = Michoacán, Mexico; NM-S = southern New Mexico; NV-E = central-eastern Nevada; NV-N = northeastern Nevada; MX-NE = Nuevo León, Mexico; OR-NE = northeastern Oregon; OR-S = southern Oregon; CA/NV-W = Sierra Nevada, California and Nevada; UT-S = southern Utah

Location	π	h	DARE-ADJ	SIZE	PROX	ISO*	LAT	POP-SIZE	MAX-NOW
AZ	0.0022	0.889	3.38	18652	65.2	2599	35.13	63045	0.764
BC	0.0019	0.778	5.09	6092	2543.7	25439	50.77	31007	0.484
ID	0.0031	0.889	9.54	15177	9573.8	49159	44.81	144790	0.56
MX-S	0.0006	0.485	3.09	181	25.1	2692	19.42	558	0.336
NM-S	0.0024	0.879	5.14	4184	14	1419	32.76	21507	0.784
NV-E	0.0017	0.802	5.28	176	82.3	6976	39.1	928	0.323
NV-N	0.0016	0.709	4.86	817	202.5	11864	41.79	3972	0.5
MX-NE	0.0024	0.727	9.63	971	13.6	1142	24.65	9355	0.548
OR-NE	0.0030	0.756	8.21	38547	2607.8	15260	45.29	316471	0.797
OR-S	0.0026	0.894	3.54	45912	1522.2	20697	42.99	162527	0.739
CA/NV-W	0.0013	0.628	2.39	15130	936.5	15629	37.79	36161	0.67
UT-S	0.0027	0.894	4.8	4969	1724.8	17759	37.84	23853	0.599

* high value represents less isolation

Table 2.2: General Linear Model statistics with nucleotide diversity (π) from 12 localities as dependent variable. B replaces POPSIZE with MAXNOW niche model estimate. Variance inflation factor (VIF) measures collinearity among independent variables using. Mallow's C_p determines

Model	Dependent variable	Estimate	Std. Error	t	*p*	VIF	Adj. R^2	Mallow's C_p
A - Full	DAREADJ	1.41E-04	6.40E-05	2.211	0.069	*1.405*	0.651	6.0
Pop. size	POPSIZE *	2.53E-04	9.26E-05	2.733	**0.034**	*1.937*		
	PROX *	-4.39E-05	1.72E-04	-0.255	0.807	8.902		
	ISO	-1.98E-09	2.31E-08	-0.086	0.935	5.774		
	LAT	1.22E-05	2.56E-05	0.477	0.651	*2.958*		
A - Best fit	DAREADJ	1.38E-04	4.69E-05	2.945	**0.016**	*1.074*	0.755	0.320
Pop. size	POPSIZE *	2.46E-04	5.78E-05	4.265	**0.002**	*1.074*		
B - Full	DAREADJ	1.73E-04	7.70E-05	2.246	0.066	*2.262*	0.624	7.0
Maxent	MAXNOW	2.55E-03	8.72E-04	2.927	**0.026**	*1.314*		
	PROX *	-2.37E-08	2.25E-07	-0.105	0.920	23.58		
	ISO	1.28E-08	4.71E-08	0.271	0.796	26.66		
	LAT	1.23E-05	2.60E-05	0.472	0.472	*3.376*		
B - Best fit	DAREADJ	1.76E-04	4.59E-05	3.839	**0.005**	*1.023*	0.753	1.255
Maxent	MAXNOW	2.48E-04	6.87E-05	3.613	**0.007**	*1.034*		
	PROX *	8.69E-04	4.99E-05	1.741	0.120	*1.057*		

* Log-normal transformation, **bold** = statistically significant (α = 0.05), *italic* VIF < 5 (cutoff)

Figure 2.1: ImageJ graph used for patch size, isolation, and proximity estimates. The population patch is in the center surrounded by neighboring patches within a buffer of 500 km in diameter.

Figure 2.2: Partial residual plot for habitat suitability estimate (MAXNOW) predicting population sizes in the presence of proximity (PROX) and territory density (DAREADJ) estimates.

Figure 2.3: Simple regression plot of nucleotide diversity index (π) over integrated independent variable of population size (POPSIZE) (A). Residual plot from regression A over observed territory density (DAREADJ) estimates (B). Residual plot from regression A over observed patch sizes (SIZE) (C).

Figure 2.4: Partial residual plots of territory density (DAREADJ; A) and habitat suitability (MAXNOW; B). Both are significant predictors of nucleotide diversity (π).

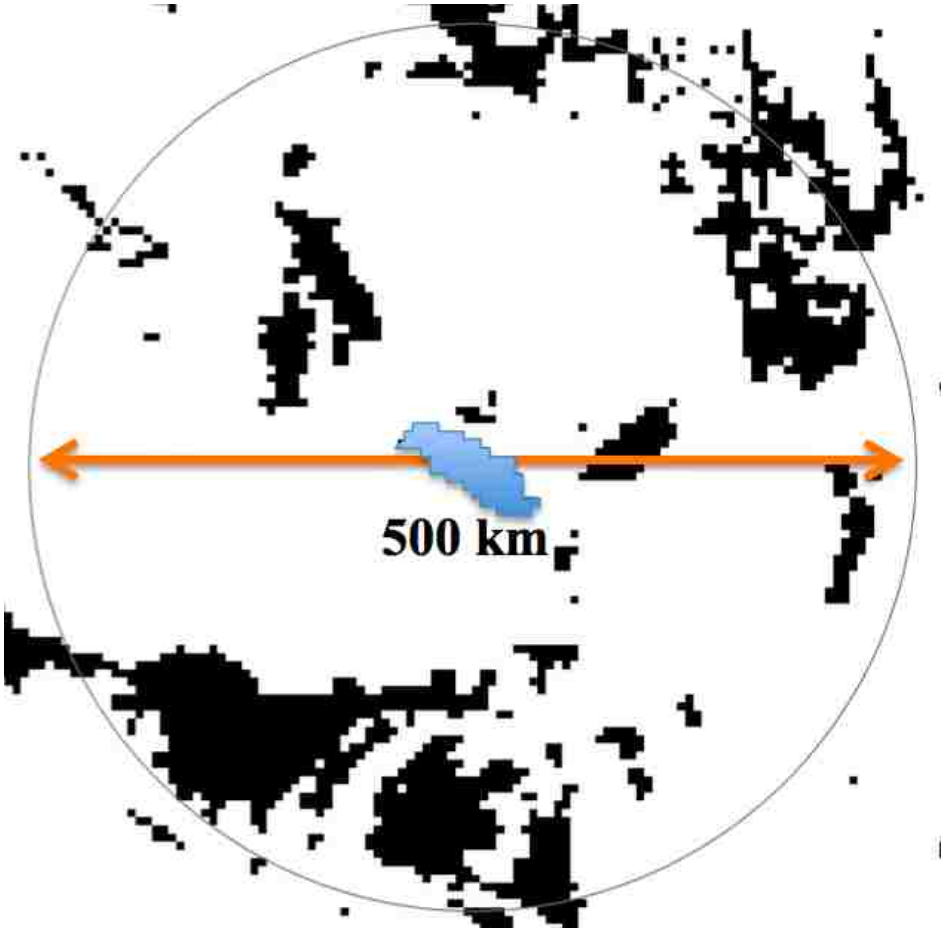

Figure 2.1

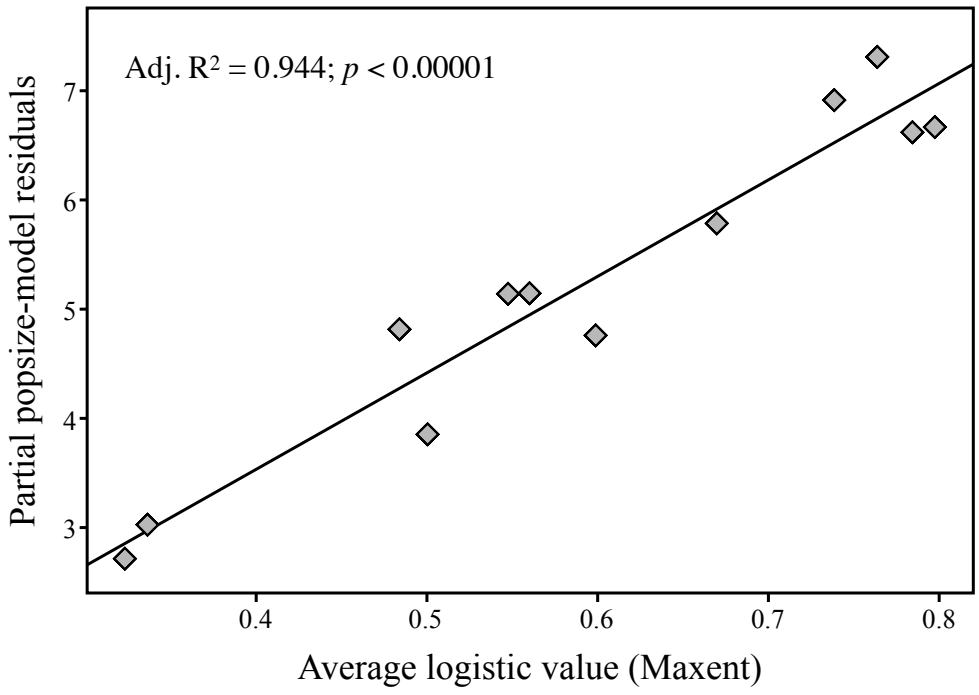
Adj. R² = 0.944; p < 0.00001
Partial popsize-model residuals
Average logistic value (Maxent)
3
4
5
6
7
0.4
0.5
0.6
0.7
0.8

Figure 2.2

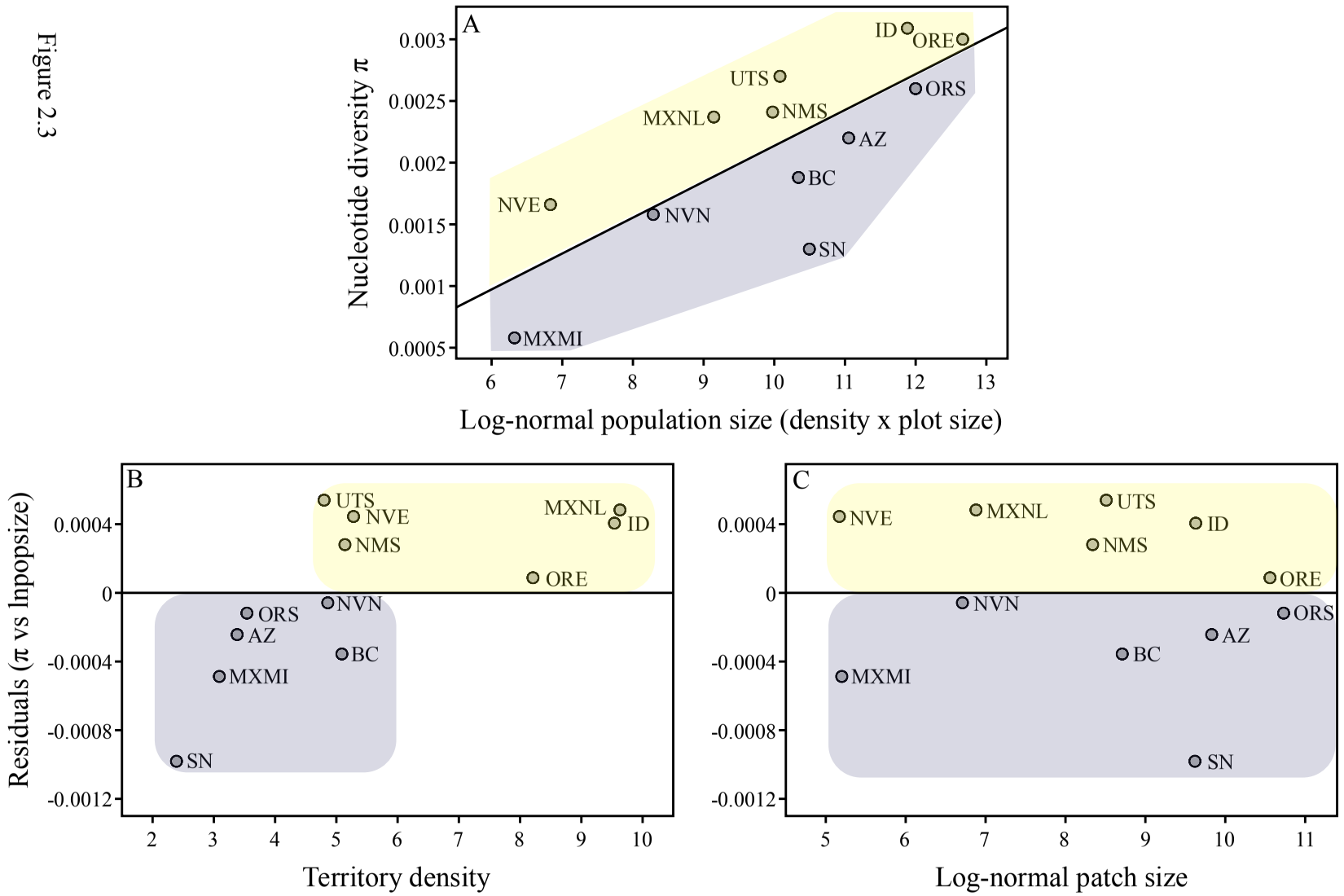
A
Nucleotide diversity π
0.003
0.0025
0.002
0.0015
0.001
0.0005
ID
ORE
UTS
ORS
MXNL
NMS
AZ
BC
NVE
NVN
SN
MXMI
6
7
8
9
10
11
12
13
Log-normal population size (density x plot size)
B
Residuals (π vs lnpopsize)
0.0004
0
-0.0004
-0.0008
-0.0012
UTS
NVE
MXNL
ID
NMS
ORE
ORS
NVN
AZ
BC
MXMI
SN
2
3
4
5
6
7
8
9
10
Territory density
C
0.0004
0
-0.0004
-0.0008
-0.0012
NVE
MXNL
UTS
ID
NMS
ORE
NVN
ORS
AZ
BC
MXMI
SN
5
6
7
8
9
10
11
Log-normal patch size

Figure 2.3

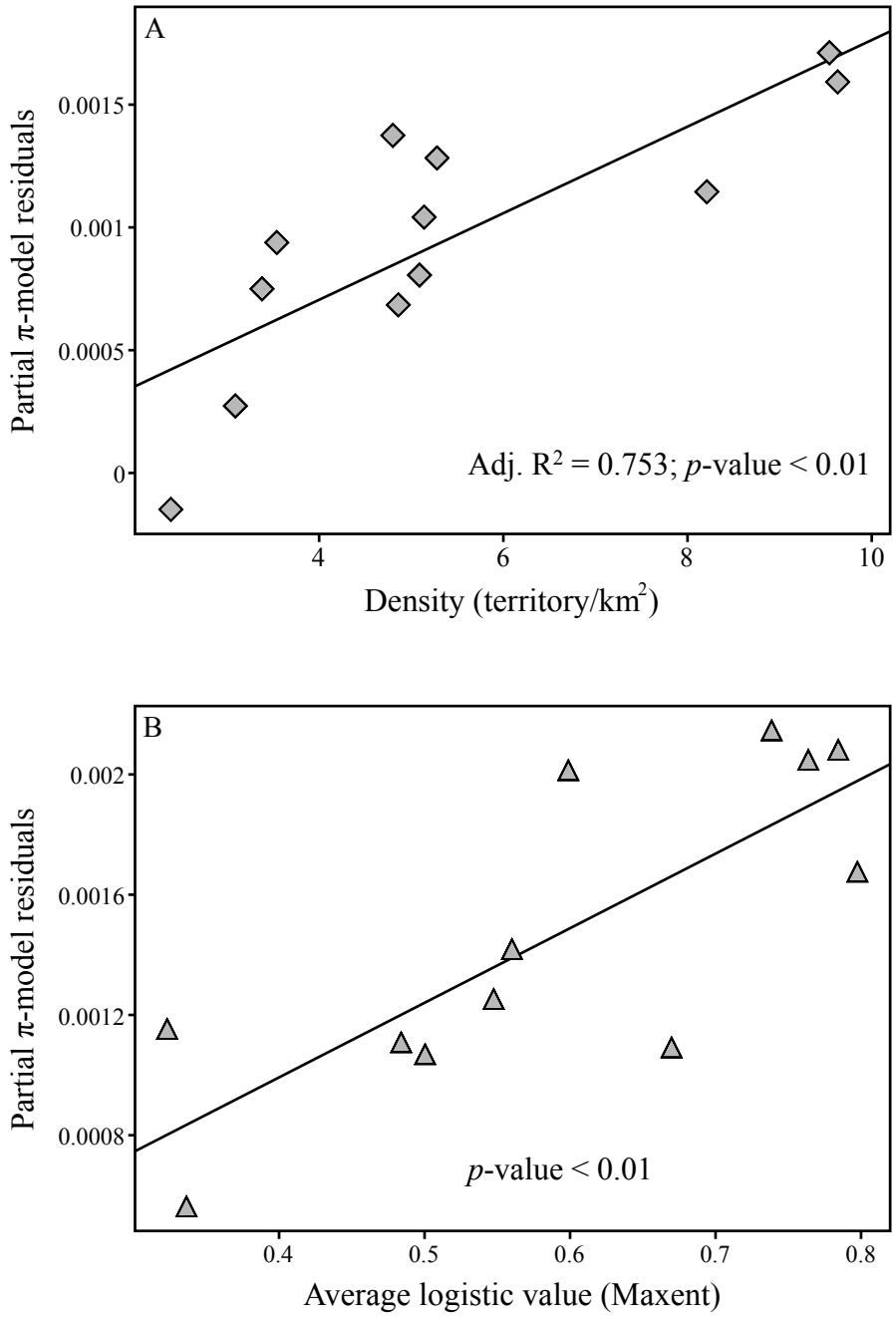
A
Partial π-model residuals
0.0015
0.001
0.0005
0
Adj. R2 = 0.753; p-value < 0.01
4
6
8
10
Density (territory/km2)
B
Partial π-model residuals
0.002
0.0016
0.0012
0.0008
p-value < 0.01
0.4
0.5
0.6
0.7
0.8
Average logistic value (Maxent)

Figure 2.4

CHAPTER 3

CONCLUSION

Genetic consequences of the biology and life history of migratory Flammulated Owls (*Otus flammeolus*) appear to be unequivocal at first. The physiological and morphological tools for long-distance mobility to track abundant food resources during migration (McCallum 1994a; Oleyar et al. 2003) and the limited number of records reporting natal site-fidelity would indicate high levels of gene flow across the range (Cadahía et al. 2009). We indeed observed panmixia among most populations using the mitochondrial marker ATPase 8 & 6 with the exception of a disjunct group inhabiting the Sierra Madre Oriental mountain range in northeastern Mexico in the state of Nuevo León. Despite small genetic differences among all haplotypes in our study, the separation over an extended period of time, and a subsequent accumulation of private haplotypes signified drastically lower gene flow to and from Nuevo León (Höglund et al. 2009), a fact validated by coalescent analysis using Migrate-n 3.0 (Beerli 2006) and significant pairwise F_{ST} values (Barrowclough 1980).

However, the propensity for far reaching gene flow and migration in the Flammulated Owl raised questions about the reasons for the Sierra Madre Oriental range containing a unique population and the barriers limiting gene flow to and from northeastern Mexico. One major force in divergence of populations and subspecies of migratory birds has been the evolution of different migration routes (Joseph et al. 2003; Ruegg et al. 2006). Separated eastern (McCallum 1994b) and western routes with the

former supplying Nuevo León and the latter contributing to populations in the United States and Canada in addition to dispersing juveniles following a familiar dispersal route would elucidate the population divergence. Another explanation may lie in the unique landscape characteristics of Nuevo León (Muñoz-Fuentes et al. 2009). As our landscape study has shown, proximity among populations was less responsible for the distribution of genetic diversity than patch or population sizes at each locality (Table 2.2). Flammulated Owls from northwestern Mexico were found on some of the smallest patches in the entire study (Table 2.1), and small patches have the tendency to receive less immigrants than large ones (Bowler and Benton 2005; Ortego et al. 2008). This fact was corroborated by relatively low immigration rates measured by Migrate-n (Fig. 1.4). The emigration estimate from Nuevo León was even smaller than immigration. Since Flammulated Owls show high levels of site fidelity among successful adults in following years (Arsenault et al. 2005), having the highest territory density estimate for all localities and an intermediate habitat suitability value in Nuevo León may indicate good quality resources birds prefer in subsequent years (Vandewoestijne et al. 2008). A similar genetic pattern with a separated population along the Sierra Madre Oriental, but a much stronger signal of population expansion into the United States and Canada was recovered in a study on MacGillivray's Warblers (Milá et al. 2000). However, no landscape genetic analyses were provided to make comparisons with our species. The results obtained here underline the importance of combining historical perspectives obtained from phylogeographic and population genetic studies with landscape genetic approaches to

obtain a more complete picture of population histories in taxa (Grant Hokit et al. 2010; Porlier et al. 2009).

The one similarity between our results from population genetics and landscape procedures was independently acquired indicators of high levels of migration. According to genetic measures of isolation-by-distance (Holsinger and Mason-Gamer 1996; Slatkin 1993), proportions of private haplotypes (Goodacre et al. 2005), and F_{ST} values (Wright 1969), gene flow was generally very high with one exception (Nuevo León). Comparing metapopulation dynamics with the distribution of genetic diversity, none of the distance-related independent variables of proximity to neighboring patches, isolation, and latitude predicted geographic patterns of diversity indices. It appeared that remote patches did not suffer the genetic consequences of isolation but rather of patch sizes, which we construed as evidence of wide-ranging migration (Esler 2000).

Due to conservation concerns for rare or threatened species, genetic consequences of small patch sizes have received the most attention and debate in metapopulation studies (Simberloff and Abele 1976). Small population sizes were generally correlated with lower levels of genetic diversity (Frankham 1996; White and Searle 2007) resulting in higher susceptibility to disease (Whiteman et al. 2006) and decreased fecundity (Campbell et al. 2010). Levels of inbreeding in a fragmented landscape structure (Saccheri et al. 1998), habitat quality estimation in patches of various sizes and their effects on population densities (García et al. 2007), and ecological traits of habitat patches and corridors as predictors of connectivity (Grant Hokit et al. 2010) were all studied in a conservation framework. Unfortunately, few empirical studies have focused

on common and mobile taxa or examined landscape genetics across large distributions. One regional metapopulation study on the Lesser Kestrel (*Falco naumanni*) was able to prove reduced genetic diversity and immigration in smaller subpopulations (Ortego et al. 2008). Similarly to the study conducted here, they hypothesized a smaller chance of individual dispersers finding small patches throughout the landscape (Bowler and Benton 2005). A number of vertebrate taxa did confirm metapopulation characteristics based on genetic variation in regional samples (García et al. 2007; Gebremedhin et al. 2009; Muñoz-Fuentes et al. 2009), but this distribution-wide approach implementing ENMs to predict the distribution and individual suitable patches, population density estimates from the field, and genetic diversity indices is unique.

LITERATURE CITED

Anderson, T. W., and D. A. Darling. 1954. A test of goodness of fit. Journal of the American Statistical Association 49:765-769.

Antolin, M. F., L. T. Savage, and R. J. Eisen. 2006. Landscape features influence genetic structure of black-tailed prairie dogs (*Cynomys ludovicianus*). Landscape Ecology 21:867-875.

Arsenault, D. P. 2007. Distribution and density of Flammulated Owls in western New Mexico. NMOS Bulletin 35:41-53.

Arsenault, D. P., P. B. Stacey, and G. A. Hoelzer. 2002. No extra-pair fertilization in Flammulated Owls despite aggregated nesting. Condor 104:197-201.

—. 2005. Mark-recapture and DNA fingerprinting data reveal high breeding-site fidelity, low natal philopatry, and low levels of genetic population differentiation in Flammulated Owls (*Otus flammeolus*). Auk 122:329-337.

Avise, J. C. 2000, Phylogeography: The history and formation of species. Cambridge, MA, Harvard University Press.

Avise, J. C., and D. Walker. 1998. Pleistocene phylogeographic effects on avian populations and the speciation process. Proceedings of the Royal Society of London Series B-Biological Sciences 265:457-463.

Ball, R. M., and J. C. Avise. 1992. Mitochondrial-DNA phylogeographic differentiation among avian populations and the evolutionary significance of subspecies. Auk 109:626-636.

Bandelt, H.-J., P. Forster, and A. Rohl. 1999. Median-joining networks for inferring intraspecific phylogenies. Molecular Biology and Evolution 16:37-48.

Barnes, K. P., and J. R. Belthoff. 2008. Probability of detection of Flammulated Owls using nocturnal broadcast surveys. Journal of Field Ornithology 79:321-328.

Barrowclough, G. F. 1980. Gene flow, effective population sizes, and genetic variance components in birds. Evolution 34:789-798.

Barrowclough, G. F., J. G. Groth, L. A. Mertz, and R. J. Gutierrez. 2006. Genetic structure of Mexican Spotted Owl (*Strix occidentalis lucida*) populations in a fragmented landscape. Auk 123:1090-1102.

Bartlein, P. J., K. H. Anderson, P. M. Anderson, M. E. Edwards, C. J. Mock, R. S. Thompson, R. S. Webb et al. 1998. Paleoclimate simulations for North America over the past 21,000 years: features of the simulated climate and comparisons with paleoenvironmental data. Quaternary Science Reviews 17:549-585.

Bech, N., J. Boissier, S. Drovetski, and C. Novoa. 2009. Population genetic structure of rock ptarmigan in the 'sky islands' of French Pyrenees: implications for conservation. Animal Conservation 12:138-146.

Beerli, P. 2006. Comparison of Bayesian and maximum-likelihood inference of population genetic parameters. Bioinformatics 22:341-345.

Beerli, P., and J. Felsenstein. 2001. Maximum likelihood estimation of a migration matrix and effective population sizes in n subpopulations by using a coalescent approach. PNAS 98:4563-4568.

Bender, D. J., L. Tischendorf, and L. Fahrig. 2003. Using patch isolation metrics to predict animal movement in binary landscapes. Landscape Ecology 18:17-39.

Bermingham, E., and C. Moritz. 1998. Comparative phylogeography: concepts and applications. Molecular Ecology 7:367-369.

Best, A. S., K. Johst, T. Münkemüller, and J. M. J. Travis. 2007. Which species will succesfully track climate change? The influence of intraspecific competition and density dependent dispersal on range shifting dynamics. Oikos 116:1531-1539.

Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews 80:205-225.

Breusch, T. S. 1979. Testing for autocorrelation in dynamic linear models. Australian Economics Papers 17:334-355.

Breusch, T. S., and A. R. Pagan. 1979. A simple test for heteroscedasticity and random coefficient variation. Econometrica 47:1287-1294.

Briles, C. E., C. Whitlock, P. J. Bartlein, and P. Higuera. 2008. Regional and local controls on postglacial vegetation and fire in the Siskiyou Mountains, northern California, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 265:159-169.

Brito, P. H. 2005. The influence of Pleistocene glacial refugia on Tawny Owl genetic diversity and phylogeography in western Europe. Molecular Ecology 14:3077-3094.

Brommer, J. E., L. Gustafsson, H. Pietiäinen, and J. Merilä. 2004. Single-generation estimates of individual fitness as proxies for long-term genetic contribution. The American Naturalist 163:505-517.

Brunsfeld, S., J. Sullivan, D. Soltis, and P. Soltis. 2001. Comparative phylogeography of northwestern North America: A synthesis, Pages 319-339 *in* J. Silverton, and J. Antonovics, eds. Integrating ecological and evolutionary processes in a spatial context. Oxford, Blackwell Science.

Burg, T. M., A. J. Gaston, K. Winker, and V. L. Friesen. 2005. Rapid divergence and postglacial colonization in western North American Steller's jays (Cyanocitta stelleri). Molecular Ecology 14:3745-3755.

Cadahía, L., P. López-López, V. Urios, Á. Soutullo, and J. J. Negro. 2009. Natal dispersal and recruitment of two Bonelli's Eagles *Aquila fasciata*: a four-year satellite tracking study. Acta Ornithologica 44:193-198.

Cadahía, L., J. Negro, and V. Urios. 2007. Low mitochondrial DNA diversity in the endangered Bonelli's Eagle (*Hieraaetus fasciatus*) from SW Europe (Iberia) and NW Africa. Journal of Ornithology 148:99-104.

Campbell, G., L. R. Noble, D. Rollinson, V. R. Southgate, J. P. Webster, and C. S. Jones. 2010. Low genetic diversity in a snail intermediate host (*Biomphalaria pfeifferi* Krass, 1848) and schistosomiasis transmission in the Senegal River Basin. Molecular Ecology 19:241-256.

Clegg, S. M., J. F. Kelly, M. Kimura, and T. B. Smith. 2003. Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a

Neotropical migrant, Wilson's Warbler (*Wilsonia pusilla*). Molecular Ecology 12:819-830.

Clement, M., D. Posada, and K. A. Crandall. 2000. TCS: a computer program to estimate gene genealogies. Molecular Ecology 9:1657-1659.

Cordellier, M., and M. Pfenninger. 2009. Inferring the past to predict the future: climate modelling predictions and phylogeography for the freshwater gastropod *Radix balthica* (Pulmonata, Basommatophora). Molecular Ecology 18:534-544.

Cracraft, J. 1982. Geographic differentiation, cladistics, and vicariance biogeography: reconstructing the tempo and mode of evolution. American Zoologist 22:411-424.

Craney, T. A., and J. G. Surles. 2002. Model-dependent variance inflation factor cutoff values. Quality Engineering 14:391-403.

del Hoyo, J., A. Elliott, and J. Sargatal. 1999, Barn-owls to Hummingbirds: Handbook of birds of the world, v. 5. Barcelona, Lynx Edicions.

Ditto, A. M., and J. K. Frey. 2007. Effects of ecogeographic variables on genetic variation in montane mammals: implications for conservation in a global warming scenario. Journal of Biogeography 34:1136-1149.

Drummond, A. J., and A. Rambaut. 2003. BEAST v1.0. Available from http://evolve.zoo.ox.ac.uk/beast/.

Drummond, A. J., A. Rambaut, B. Shapiro, and O. G. Pybus. 2005. Bayesian coalescent inference of past population dynamics from molecular sequences. Molecular Biology and Evolution 22:1185-1192.

Dunham, S., L. Butcher, D. A. Charlet, and J. M. Reed. 1996. Breeding range and conservation of Flammulated Owls (*Otus flammeolus*) in Nevada. Journal of Raptor Research 30:189-193.

Dupanloup, I., S. Schneider, and L. Excoffier. 2002. A simulated annealing approach to define the genetic structure of populations. Molecular Ecology 11:2571-2581.

Durbin, J., and G. S. Watson. 1971. Testing for serial correlation in least squares regression III. Biometrika 58:1-19.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129-151.

Emerick, C. M., and R. A. Duncan. 1982. Age progressive volcanism in the Comores Archipelago, western Indian Ocean and implications for Somali plate tectonics. Earth and Planetary Science Letters 60:415-428.

Esler, D. 2000. Applying metapopulation theory to conservation of migratory birds. Conservation Biology 14:366-372.

Evans, M. E. K., S. A. Smith, R. S. Flynn, and M. J. Donoghue. 2009. Climate, niche evolution, and diversification of the "bird-cage" evening primroses (*Oenothera*, sections *Anogra* and *Kleinia*). The American Naturalist 173:225-240.

Ewens, W. J. 1972. The sampling theory of selectively neutral alleles. Theoretical Population Biology 3:87-112.

Excoffier, L., 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.

Excoffier, L., P. E. Smouse, and J. M. Quattro. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial restriction data. Genetics 131:479-491.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38-49.

Frankham, R. 1996. Relationship of genetic variation to population size in wildlife. Conservation Biology 10:1500-1508.

Franzén, M., and S. G. Nilsson. 2010. Both population size and patch quality affect local extinctions and colonizations. Proceedings of the Royal Society B: Biological Sciences 277:79-85.

Fry, A. J., and R. M. Zink. 1998. Geographic analysis of nucleotide diversity and song sparrow (Aves: Emberizidae) population history. Molecular Ecology 7:1303-1313.

Fu, Y. X. 1997. Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. Genetics 147:915-925.

Fuchs, J., J. M. Pons, S. M. Goodman, V. Bretagnolle, M. Melo, R. C. K. Bowie, D. Currie et al. 2008. Tracing the colonization history of the Indian Ocean scops-owls (Strigiformes : Otus) with further insight into the spatio-temporal origin of the Malagasy avifauna. Bmc Evolutionary Biology 8.

García, J., S. Suárez-Seoane, D. Miguélez, P. E. Osborne, and C. Zumalacárregui. 2007. Spatial analysis of habitat quality in a fragmented population of little bustard (*Tetrax tetrax*): Implications for conservation. Biological Conservation 137:45-56.

Gebremedhin, B., G. F. Ficetola, S. Naderi, H.-R. Rezaei, C. Maudet, D. Rioux, G. Luikart et al. 2009. Combining genetic and ecological data to assess the conservation status of the endangered Ethiopian walia ibex. Animal Conservation 12:89-100.

Godfrey, L. G. 1978. Testing against general autoregressive and moving average error models when the regressors include lagged dependent variables. Econometrica 46:1293-1302.

Godsoe, W. 2010. Regional variation exaggerates ecological divergence in niche models. Systematic Biology:DOI 10.1093/sysbio/syq1005.

Goodacre, S., A. Helgason, J. Nicholson, L. Southam, L. Ferguson, E. Hickey, E. Vega et al. 2005. Genetic evidence for a family-based Scandinavian settlement of Shetland and Orkney during the Viking periods. Heredity 95:129-135.

Gotelli, N. J. 1991. Metapopulation models: the rescue effect, the propagule rain, and the core-satellite hypothesis. American Naturalist 138:768-776.

Grant Hokit, D., M. Ascunce, J. Ernst, L. Branch, and A. Clark. 2010. Ecological metrics predict connectivity better than geographic distance. Conservation Genetics 11:149-159.

Grant, W. S., and B. W. Bowen. 1998. Shallow population histories in deep evolutionary lineages of marine fishes: insights from sardines and anchovies and lessons for conservation. Journal of Heredity 89:415-426.

Greenberg, R. S., P. J. Cordero, S. Droege, and R. C. Fleischer. 1998. Morphological adaptation with no mitochondrial DNA differentiation in the coastal plain swamp sparrow. Auk 115:706-712.

Guindon, S., and O. Gascuel. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Systematic Biology 52:696-704.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147-186.

Hale, K. A., and J. V. Briskie. 2009. Rapid recovery of an island population of the threatened South Island saddleback *Philesturnus c. carunculatus* after a pathogen outbreak. Bird Conservation International 19:239-253.

Hames, R. S., K. V. Rosenberg, J. D. Lowe, and A. A. Dhondt. 2001. Site reoccupation in fragmented landscapes: testing predictions of metapopulation theory. Journal of Animal Ecology 70:182-190.

Hanski, I. 2004. Metapopulation biology: past, present, and future, Pages 3-22 *in* I. Hanski, and O. E. Gaggiotti, eds. Ecology, genetics, and evolution of metapopulations. Burlington, MA, Elsevier Academic Press.

Hansson, B., S. Bensch, D. Hasselquist, B.-G. Lillandt, L. Wennerberg, and T. V. Schantz. 2000. Increase of genetic variation over time in a recently founded population of

great reed warblers (*Acrocephalus arundinaceus*) revealed by microsatellites and DNA fingerprinting. Molecular Ecology 9:1529-1538.

Harding, R. M. 1996. New phylogenies: an introductory look at the coalescent, Pages 15-22 *in* P. H. Harvey, A. J. L. Brown, J. M. Smith, and S. Nee, eds. New Uses for New Phylogenies. Oxford, England, Oxford University Press.

Harpending, H. C. 1994. Signature of ancient population growth in a low-resolution mitochondrial DNA mismatch distribution. Human Biology 66:591-600.

Hartl, D. L., and A. G. Clark. 1997, Principles of population genetics. Sunderland, MD, Sinauer Associates, Inc.

Hayward, G. D., P. H. Hayward, and E. O. Garton. 1993. Ecology of Boreal Owls in the northern Rocky Mountains, U.S.A. Wildlife Monographs 124:1-59.

Heled, J., and A. J. Drummond. 2008. Bayesian inference of population size history from multiple loci. BMC Evolutionary Biology 8:289.

Helgason, A., E. Hickey, S. Goodacre, V. Bosnes, K. Stefansson, R. Ward, and B. Sykes. 2001. mtDNA and the islands of the North Atlantic: estimating the proportions of norse and gaelic ancestry. American Journal of Human Genetics 68:723-737.

Hewitt, G. M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. Biological Journal of the Linnean Society 58:247-276.

—. 2000. The genetic legacy of the Quaternary ice ages. Nature 405:907-913.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965-1978.

Ho, S. Y. W., M. J. Phillips, A. Cooper, and A. J. Drummond. 2005. Time dependency of molecular rate estimates and systematic overestimation of recent divergence times. Molecular Biology and Evolution 22:1561-1568.

Ho, S. Y. W., U. Saarma, R. Barnett, J. Haile, and B. Shapiro. 2008. The effect of inappropriate calibration: Three case studies in molecular ecology. PLoS ONE 3:e1615.

Höglund, J., T. Johansson, A. Beintema, and H. Schekkerman. 2009. Phylogeography of the Black-tailed Godwit *Limosa limosa*: substructuring revealed by mtDNA control region sequences. Journal of Ornithology 150:45-53.

Holsinger, K. E., and R. J. Mason-Gamer. 1996. Hierarchical analysis of nucleotide diversity in geographically structured populations. Genetics 142:629-639.

Honnay, O., P. Endels, H. Vereecken, and M. Hermy. 1999. The role of patch area and habitat diversity in explaining native plant species richness in disturbed suburban forest patches in northern Belgium. Diversity and Distributions 5:129-141.

Hudson, R. R., D. D. Boos, and N. L. Kaplan. 1992a. A statistical test for detecting geographic subdivision. Molecular Biology and Evolution 9:138-151.

Hudson, R. R., M. Slatkin, and W. P. Maddison. 1992b. Estimation of levels of gene flow from DNA sequence data. Genetics 132:583-589.

Ibrahim, K. M., R. A. Nichols, and G. M. Hewitt. 1996. Spatial patterns of genetic variation generated by different forms of dispersal during range expansion. Heredity 77:282-291.

Jones, K. L., G. L. Krapu, D. A. Brandt, and M. V. Ashley. 2005. Population genetic structure in migratory sandhill cranes and the role of Pleistocene glaciations. Molecular Ecology 14:2645-2657.

Joseph, L., T. Wilke, and D. Alpers. 2003. Independent evolution of migration on the South American landscape in a long-distance temperate-tropical migratory bird, Swainson's flycatcher (*Myiarchus swainsoni*). Journal of Biogeography 30:925-937.

Kawecki, T. J., and R. D. Holt. 2002. Evolutionary consequences of asymmetric dispersal rates. American Naturalist 160:333-347.

Kingman, J. F. C. 1982. The coalescent. Stochastic Processes and their Applications 13:235-248.

Klicka, J., and R. M. Zink. 1997. The importance of recent ice ages in speciation: A failed paradigm. Science 277:1666-1669.

Koenker, R. 1981. A note on studentizing a test for heteroscedasticity. Journal of Econometrics 17:107-112.

Koopman, M. E., G. D. Hayward, and D. B. McDonald. 2007. High connectivity and minimal genetic structure among North American Boreal Owl (*Aegolius funereus*) populations, regardless of habitat matrix. Auk 124:690-704.

Latta, R. G., and J. B. Mitton. 1999. Historical separation and present gene flow through a zone of secondary contact in ponderosa pine. Evolution 53:769-776.

Lees, A. C., and C. A. Peres. 2008. Avian life-history determinants of local extinction risk in a hyper-fragmented neotropical forest landscape. Animal Conservation 11:128-137.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237-240.

Li, P. 1986. Range-wide patterns of allozyme variation in Douglas-fir (*Pseudotsuga menziesii*), Oregon State University, Corvallis, OR.

Linkhart, B. D. 1984. Range, activity, and habitat use by nesting Flammulated Owls in a Colorado ponderosa pine forest. M.S. thesis, Colorado State University, Fort Collins.

Lomolino, M. V., and J. H. Brown. 2009. The reticulating phylogeny of island biogeography theory. Quarterly Review of Biology 84:357-390.

Lovette, I. J. 2005. Glacial cycles and the tempo of avian speciation. Trends in Ecology & Evolution 20:57-59.

MacArthur, R. H., and E. O. Wilson. 1967, The theory of island biogeography. Princeton, NJ, Princeton University Press.

Mallows, C. L. 1973. Some comments on Cp. Technometrics 15:661-675.

Marti, C. D. 1997. Flammulated Owls (*Otus flammeolus*) breeding in deciduous forests, Pages 262-266 *in* J. R. Duncan, D. H. Johnson, and T. H. Nicholls, eds. Biology and conservation of owls of the northern hemisphere. Winnipeg, Manitoba, Canada, USDA Forest Service Gen. Tech. Rep. NC-190.

McCallum, D. A. 1994a. Flammulated Owl (*Otus flammeolus*), Pages 1-24 *in* A. Poole, and F. B. Gill, eds. The Birds of North America. Philadelphia, The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

—. 1994b. Review of technical knowledge: Flammulated Owls *in* G. D. Hayward, and J. Verner, eds. Flammulated, Boreal, and Great Gray Owls in United States: a technical conservation assessment, USDA Forest Service Gen. Tech. Rep. RM-253.

Mengel, R. M. 1970. The North American Central Plains as an isolating agent in bird speciation *in* W. Dort Jr., and J. K. Jones, eds. Pleistocene and recent environments of the Central Great Plains. Lawrence, KS, University of Kansas Press.

Mika, M. 2003. Prey base differences and reproductive output of Flammulated Owls (*Otus flammeolus*) in northern Utah. M.S. thesis, Brigham Young University, Provo.

Milá, B., D. J. Girman, M. Kimura, and T. B. Smith. 2000. Genetic evidence for the effect of a postglacial population expansion on the phylogeography of a North American songbird. Proceedings of the Royal Society B-Biological Sciences 267:1033-1040.

Milá, B., T. B. Smith, and R. K. Wayne. 2006. Postglacial population expansion drives the evolution of long-distance migration in a songbird. Evolution 60:2403-2409.

—. 2007. Speciation and rapid phenotypic differentiation in the yellow-rumped warbler *Dendroica coronata* complex. Molecular Ecology 16:159-173.

Mlíkovský, J. 1998. Two new owls (Aves: Strigidae) from the Early Miocene of the Czech Republic, with comments on the fossil history of the subfamily Striginae. Buteo 10:5-22.

Morando, M., L. J. Avila, and J. W. Sites Jr. 2003. Sampling strategies for delimiting species: genes, individuals, and populations in the *Liolaemus elongatus-kriegi* complex (Squamata: Liolaemidae) in Andean-Patagonian South America. Systematic Biology 52:159-185.

Muñoz-Fuentes, V., C. T. Darimont, R. K. Wayne, P. C. Paquet, and J. A. Leonard. 2009. Ecological factors drive differentiation in wolves from British Columbia. Journal of Biogeography 36:1516-1531.

Nei, M. 1973. Analysis of gene diversity in subdivided populations. PNAS 70:3321-3323.

—. 1982. Evolution of human races at the gene level, Pages 167-181 *in* B. Bonne-Tamir, T. Cohen, and R. M. Goodman, eds. Human genetics, Part A: the unfolding genome. New York, Alan R. Liss.

—. 1987, Molecular evolutionary genetics. New York, NY, Columbia University Press.

Nei, M., and W. H. Li. 1979. Mathematical model for studying genetic variation in terms of restriction endonucleases. Proceedings of the National Academy of Sciences of the United States of America 76:5269-5273.

O'Keefe, K., U. Ramakrishnan, M. Van Tuinen, and E. A. Hadly. 2009. Source-sink dynamics structure a common montane mammal. Molecular Ecology 18:4775-4789.

Ochoa-Gaona, S., and M. González-Espinosa. 2000. Land use and deforestation in the highlands of Chiapas, Mexico. Applied Geography 20:17-42.

Ohlson, J., J. Fjeldsa, and P. G. P. Ericson. 2008. Tyrant flycatchers coming out in the open: phylogeny and ecological radiation of Tyrannidae (Aves, Passeriformes). Zoologica Scripta 37:315-335.

Oleyar, M. D., C. D. Marti, and M. Mika. 2003. Vertebrate prey in the diet of Flammulated Owls in Northern Utah. Journal of Raptor Research.

Ortego, J., J. M. Aparicio, P. J. Cordero, and G. Calabuig. 2008. Individual genetic diversity correlates with the size and spatial isolation of natal colonies in a bird metapopulation. Proceedings of the Royal Society B: Biological Sciences 275:2039-2047.

Ortego, J., G. Calabuig, P. J. Cordero, and J. M. Aparicio. 2007. Egg production and individual genetic diversity in lesser kestrels. Molecular Ecology 16:2383-2392.

Otto-Bliesner, B. L., E. C. Brady, G. Clauzet, R. Tomas, S. Levis, and Z. Kothavala. 2006. Last glacial maximum and holocene climate in CCSM3. Journal of Climate 19:2526-2544.

Panchal, M., and M. A. Beaumont. 2007. The automation and evaluation of nested clade phylogeographic analysis. Evolution 61:1466-1480.

Parolo, G., G. Rossi, and A. Ferrarini. 2008. Toward improved species niche modelling: *Arnica montana* in the Alps as a case study. Journal of Applied Ecology 45:1410-1418.

Pearson, R. G., C. J. Raxworthy, M. Nakamura, and A. T. Peterson. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34:102-117.

Pease, K. M., A. H. Freedman, J. P. Pollinger, J. E. Mccormack, W. Buermann, J. Rodzen, J. Banks et al. 2009. Landscape genetics of California mule deer (*Odocoileus hemionus*): the roles of ecological and historical factors in generating differentiation. Molecular Ecology 18:1848-1862.

Peterson, A. T. 2001. Predicting species' geographic distributions based on ecological niche modeling. Condor 103:599-605.

Peterson, A. T., M. Papeş, and M. Eaton. 2007. Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. Ecography 30:550-560.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190:231-259.

Porlier, M., M. Bélisle, and D. Garant. 2009. Non-random distribution of individual genetic diversity along an environmental gradient. Philosophical Transactions of the Royal Society B: Biological Sciences 364:1543-1554.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652-661.

Pybus, O. G., A. Rambaut, and P. H. Harvey. 2000. An integrated framework for the inference of viral population history from reconstructed genealogies. Genetics 155:1429-1437.

Rand, A. L. 1948. Glaciation, an isolating factor in speciation. Evolution 2:314-321.

Rehfeldt, G. E. 1978. Genetic differentiation of Douglas-fir populations from the northern Rocky Mountains. Ecology 59:1264-1270.

Reynolds, R. T., and B. D. Linkhart. 1987. Fidelity to territory and mate in Flammulated Owls *in* R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre, eds. Biology and conservation of northern forest owls, USDA Forest Service Gen. Tech. Rep. RM-142.

Ronchetti, E., and R. G. Staudte. 1994. A robust version of Mallows's C_p. Journal of the American Statistical Association 89:550-559.

Rousset, F. 1997. Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. Genetics 145:1219-1228.

Rozas, J., J. C. Sanchez-DelBarrio, X. Messeguer, and R. Rozas. 2003. DnaSP, DNA polymorphism analyses by the coalescent and other methods. Bioinformatics 19:2496-2497.

Ruedi, M., and V. Castella. 2003. Genetic consequences of the ice ages on nurseries of the bat Myotis myotis: a mitochondrial and nuclear survey. Molecular Ecology 12:1527-1540.

Ruegg, K. C., R. J. Hijmans, and C. Moritz. 2006. Climate change and the origin of migratory pathways in the Swainson's thrush, *Catharus ustulatus*. Journal of Biogeography 33:1172-1182.

Saccheri, I., M. Kuussaari, M. Kankare, P. Vikman, W. Fortelius, and I. Hanski. 1998. Inbreeding and extinction in a butterfly metapopulation. Nature 392:491-494.

Sattler, T., F. Bontadina, A. H. Hirzel, and R. Arlettaz. 2007. Ecological niche modelling of two cryptic bat species calls for a reassessment of their conservation status. Journal of Applied Ecology 44:1188-1199.

Schluter, D. 1993. Adaptive radiation in sticklebacks: size, shape, and habitat use efficiency. Ecology 74:699-709.

Schwarz, G. 1978. Estimating the dimension of a model. Annals of Statistics 6:461-464.

Seppa, P., and A. Laurila. 1999. Genetic structure of island populations of the anurans *Rana temporaria* and *Bufo bufo*. Heredity 82:309-317.

Simberloff, D. S., and L. G. Abele. 1976. Island biogeography theory and conservation practice. Science 191:285-286.

Simberloff, D. S., and E. O. Wilson. 1969. Experimental zoogeography of islands: the colonization of empty islands. Ecology 50:278-296.

Slatkin, M. 1985. Gene flow in natural populations. Annual Review of Ecology and Systematics 16:393-430.

—. 1993. Isolation by distance in equilibrium and non-equilibrium populations. Evolution 47:264-279.

Slatkin, M., and R. R. Hudson. 1991. Pairwise comparisons of mitochondrial DNA sequences in stable and exponentially growing populations. Genetics 129:555-562.

Smith, F. A., D. L. Crawford, L. E. Harding, H. M. Lease, I. W. Murray, A. Raniszewski, and K. M. Youberg. 2009. A tale of two species: Extirpation and range expansion

during the late Quaternary in an extreme environment. Global and Planetary Change 65:122-133.

Sorenson, M. D., and T. W. Quinn. 1998. Numts: A challenge for avian systematics and population biology. Auk 115:214-221.

Spellman, G. M., and J. Klicka. 2006. Testing hypotheses of Pleistocene population history using coalescent simulations: phylogeography of the pygmy nuthatch (*Sitta pygmaea*). Proceedings of the Royal Society B: Biological Sciences 273:3057-3063.

—. 2007. Phylogeography of the White-breasted Nuthatch (*Sitta carolinensis*): diversification in North American pine and oak woodlands. Molecular Ecology 16:1729-1740.

Spellman, G. M., B. R. Riddle, and J. Klicka. 2007. Phylogeography of the mountain chickadee (*Poecile gambeli*): diversification, introgression, and expansion in response to Quaternary climate change. Molecular Ecology 16:1055-1068.

Stenzler, L. M., C. A. Makarewich, A. Coulon, D. R. Ardia, I. J. Lovette, and D. W. Winkler. 2009. Subtle edge-of-range genetic structuring in transcontinentally distributed North American Tree Swallows. Condor 111:470-478.

Stine, R. A. 1995. Graphical interpretation of variance inflation factors. The American Statistician 49:53-56.

Stockman, A. K., and J. E. Bond. 2007. Delimiting cohesion species: extreme population structuring and the role of ecological interchangeability. Molecular Ecology 16:3374-3392.

Strong, W. L., and L. V. Hills. 2005. Late-glacial and Holocene palaeovegetation zonal reconstruction for central and north-central North America. Journal of Biogeography 32:1043-1062.

Strubbe, D., and E. Matthysen. 2009. Establishment success of invasive ring-necked and monk parakeets in Europe. Journal of Biogeography 36:2264-2278.

Suárez-Seoane, S., E. L. GarcÌa de la Morena, M. B. Morales Prieto, P. E. Osborne, and E. de Juana. 2008. Maximum entropy niche-based modelling of seasonal changes in little bustard (*Tetrax tetrax*) distribution. Ecological Modelling 219:17-29.

Tajima, F. 1983. Evolutionary relationship of DNA sequences in finite populations. Genetics 105:437-460.

—. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123:585-595.

Taylor, S. S., I. G. Jamieson, and G. P. Wallis. 2007. Historic and contemporary levels of genetic variation in two New Zealand passerines with different histories of decline. Journal of Evolutionary Biology 20:2035-2047.

Templeton, A. R., E. Routman, and C. A. Phillips. 1995. Separating population structure from population history: A cladistic analysis of the geographical distribution of mitochondrial DNA haplotypes in the tiger salamander, *Ambystoma tigrinum*. Genetics 140:767-782.

Toro, M. A., and A. Caballero. 2005. Characterization and conservation of genetic diversity in subdivided populations. Philosophical Transactions: Biological Sciences 360:1367-1378.

Van Devender, T. R. 1990. Late Quaternary vegetation and climate of the Chihuahuan desert, United States and Mexico, Pages 104-133 *in* J. L. Betancourt, T. R. Van Devender, and P. S. Martin, eds. Packrat middens: The last 40,000 years of biotic change. Tucson, The University of Arizona Press.

Van Devender, T. R., J. L. Betancourt, and M. Wimberly. 1984. Biogeographic implications of a packrat midden sequence from the Sacramento Mountains, south-central New Mexico. Quaternary Research 22:344-360.

van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Vandewoestijne, S., N. Schtickzelle, and M. Baguette. 2008. Positive correlation between genetic diversity and fitness in a large, well-connected metapopulation. BMC Biology 6:1-11.

Vickery, P. D., M. L. Hunter, Jr., and J. V. Wells. 1992. Is density an indicator of breeding success? Auk 109:706-710.

Wagner, C. E., and A. R. McCune. 2009. Contrasting patterns of spatial genetic structure in sympatric rock-dwelling cichlid fishes. Evolution 63:1312-1326.

Waltari, E., R. J. Hijmans, A. T. Peterson, Á. S. Nyári, S. L. Perkins, and R. P. Guralnick. 2007. Locating pleistocene refugia: comparing phylogeographic and ecological niche model predictions. PLoS ONE 2:1-11.

Weng, C. Y., and S. T. Jackson. 1999. Late glacial and holocene vegetation history and paleoclimate of the Kaibab Plateau, Arizona. Palaeogeography Palaeoclimatology Palaeoecology 153:179-201.

West, G. J., W. Woolfenden, J. A. Wanket, and R. S. Anderson. 2007. Late Pleistocene and Holocene Environments, Pages 11-34 *in* T. L. Jones, and K. A. Klar, eds. California prehistory: colonization, culture, and complexity. Lanham, MD, Rowman & Littlefield Publishers, Inc.

White, T. A., and J. B. Searle. 2007. Genetic diversity and population size: island populations of the common shrew, *Sorex araneus*. Molecular Ecology 16:2005-2016.

Whiteman, N. K., K. D. Matson, J. L. Bollmer, and P. G. Parker. 2006. Disease ecology in the Galápagos Hawk (*Buteo galapagoensis*): host genetic diversity, parasite load and natural antibodies. Proceedings of the Royal Society B: Biological Sciences 273:797-804.

Wilson, T. L., E. J. Johnson, and J. A. Bissonette. 2009. Relative importance of habitat area and isolation for bird occurrence patterns in a naturally patchy landscape. Landscape Ecology 24:351-360.

Woudenberg, A. M., and D. A. Kirk. 1999. COSEWIC assessment and update; status report on the Flammulated Owl *Otus flammeolus* in Canada, Pages 1-24, Committee on the Status of Endangered Wildlife in Canada.

Wright, S. 1969, Evolution and the genetics of populations Volume 2: the theory of gene frequencies. Chicago, University of Chicago Press.

Yansa, C. H., and A. C. Ashworth. 2005. Late Pleistocene palaeoenvironments of the southern Lake Agassiz Basin, USA. Journal of Quaternary Science 20:255-267.

Zhu, L., L. Li, and Z. Liang. 2009. Comparison of six statistical approaches in the selection of appropriate fish growth models. Chinese Journal of Oceanology and Limnology 27:457-467.

Zink, R. M. 1996. Comparative phylogeography in North American birds. Evolution 50:308-317.

—. 1997. Phylogeographic studies of North American birds, Pages 301-324 *in* D. P. Mindell, ed. Avian molecular evolution and systematics. San Diego, CA, Academic Press.

APPENDIX

SPECIMEN DATA

Genus	Species	Band/Tissue #	H	State	Specific Locality	Lat Long
Otus	*flammeolus*	1603-03033	**1**	AZ	Woody Ridge, 18.5 mi WSW of Flagstaff	35˚04.005N/111˚54.964W
Otus	*flammeolus*	1603-03034	**2**	AZ	Woody Ridge, 18.5 mi WSW of Flagstaff	35˚04.005N/111˚54.964W
Otus	*flammeolus*	1603-03035	**2**	AZ	Woody Ridge, 17.0 mi WSW of Flagstaff	35˚04.019N/111˚52.893W
Otus	*flammeolus*	1603-03036	**3**	AZ	Woody Ridge, 17.0 mi WSW of Flagstaff	35˚04.019N/111˚52.893W
Otus	*flammeolus*	1603-03037	**4**	AZ	Woody Ridge, 16.2 mi WSW of Flagstaff	35˚04.473N/111˚52.269W
Otus	*flammeolus*	1603-03038	**5**	AZ	A 1 Mountain, 7.8 mi W of Flagstaff	35˚14.237N/111˚44.708W
Otus	*flammeolus*	1603-03039	**5**	AZ	A 1 Mountain, 7.8 mi W of Flagstaff	35˚14.094N/111˚45.630W
Otus	*flammeolus*	1603-03040	**1**	AZ	Woody Ridge, 17.9 mi SW of Flagstaff	35˚01.218N/111˚51.641W
Otus	*flammeolus*	1603-03041	**6**	AZ	Woody Ridge, 15.4 mi SW of Flagstaff	35˚04.299N/111˚51.108W
Otus	*flammeolus*	MM564	**2**	AZ	A 1 Mountain, 7.8 mi W of Flagstaff	35˚04.299N/111˚51.108W
Otus	*flammeolus*	1513-15601	**7**	BC	Wheeler Mtn., 6.3 mi NW of Kamloops	50˚45.881N/120˚28.789W
Otus	*flammeolus*	1513-15602	**6**	BC	Wheeler Mtn., 8.2 mi NW of Kamloops	50˚45.782N/120˚31.898W
Otus	*flammeolus*	1513-15603	**5**	BC	Wheeler Mtn., 8.5 mi NW of Kamloops	50˚45.901N/120˚32.221W
Otus	*flammeolus*	1513-15604	**5**	BC	Wheeler Mtn., 8.5 mi NW of Kamloops	50˚45.901N/120˚32.221W
Otus	*flammeolus*	1513-15605	**6**	BC	Wheeler Mtn., 9.2 mi NW of Kamloops	50˚46.363N/120˚33.021W
Otus	*flammeolus*	1513-15606	**8**	BC	Wheeler Mtn., 9.2 mi NW of Kamloops	50˚46.363N/120˚33.021W
Otus	*flammeolus*	1513-15607	**5**	BC	Wheeler Mtn., 7.0 mi NW of Kamloops	50˚46.953N/120˚28.298W
Otus	*flammeolus*	1513-15608	**6**	BC	Wheeler Mtn., 7.0 mi NW of Kamloops	50˚46.442N/120˚29.577W
Otus	*flammeolus*	1513-15609	**6**	BC	Wheeler Mtn., 6.5 mi NW of Kamloops	50˚46.102N/120˚28.700W
Otus	*flammeolus*	1513-15610	**7**	BC	Wheeler Mtn., 6.6 mi NW of Kamloops	50˚46.074N/120˚28.996W
Otus	*flammeolus*	1603-03013	**13**	ID	Seid Creek, 12 mi NW of Cambridge	44˚43.440N/116˚48.174W
Otus	*flammeolus*	1603-03014	**5**	ID	Grade Creek, 16 mi NW of Cambridge	44˚47.228N/116˚48.754W
Otus	*flammeolus*	1603-03015	**14**	ID	Grade Creek, 16 mi NW of Cambridge	44˚47.131N/116˚48.633W
Otus	*flammeolus*	1603-03016	**15**	ID	Dick Ross Creek, 9.8 mi S of Bear	44˚52.965N/116˚40.035W
Otus	*flammeolus*	1603-03017	**16**	ID	Dick Ross Creek, 9.5 mi S of Bear	44˚53.157N/116˚40.249W
Otus	*flammeolus*	1603-03018	**6**	ID	Dick Ross Creek, 9.3 mi S of Bear	44˚53.454N/116˚40.495W
Otus	*flammeolus*	1603-03019	**13**	ID	Crooked River, 11.5 mi S of Bear	44˚52.252N/116˚42.639W
Otus	*flammeolus*	1603-03020	**6**	ID	Crooked River, 11 mi S of Bear	44˚52.487N/116˚42.621W
Otus	*flammeolus*	1603-03021	**5**	ID	Crooked River, 10.9 mi S of Bear	44˚52.635N/116˚42.732W

Genus	Species	Band/Tissue #	H	State	Specific Locality	Lat Long
Otus	*flammeolus*	1603-03022	**5**	ID	Seid Creek, 12 mi NW of Cambridge	44˚43.640N/116˚48.355W
Otus	*flammeolus*	MM442	**2**	Mich.	Guiramo, 9.6 mi W of Nuevo San Juan	19˚23.839N/102˚16.666W
Otus	*flammeolus*	MM443	**2**	Mich.	Guiramo, 9.5 mi W of Nuevo San Juan	19˚24.236N/102˚16.614W
Otus	*flammeolus*	MM480	**2**	Mich.	Guiramo, 9.6 mi W of Nuevo San Juan	19˚26.272N/102˚15.363W
Otus	*flammeolus*	MM481	**2**	Mich.	Guiramo, 9.6 mi W of Nuevo San Juan	19˚25.863N/102˚16.509W
Otus	*flammeolus*	MM482	**2**	Mich.	Guiramo, 8.7 mi W of Nuevo San Juan	19˚25.863N/102˚16.509W
Otus	*flammeolus*	MM483	**2**	Mich.	Guiramo, 8.2 mi W of Nuevo San Juan	19˚26.157N/102˚15.890W
Otus	*flammeolus*	JK06-525	**6**	Mich.	Guiramo, 9 mi W of Nuevo San Juan	19˚24.676N/102˚16.136W
Otus	*flammeolus*	MM484	**6**	Mich.	Guiramo, 8.9 mi W of Nuevo San Juan	19˚24.921N/102˚16.252W
Otus	*flammeolus*	MM485	**2**	Mich.	Guiramo, 8.9 mi W of Nuevo San Juan	19˚25.217N/102˚16.167W
Otus	*flammeolus*	MM486	**2**	Mich.	Guiramo, 8.8 mi W of Nuevo San Juan	19˚25.575N/102˚16.159W
Otus	*flammeolus*	MX01	**6**	Mich.	Mountain range near Morelia	
Otus	*flammeolus*	MX02	**6**	Mich.	Mountain range near Morelia	
**Otus*	*flammeolus*	NM8380	**2**	NM	Oso Ridge, 16 mi WSW of Grants	
**Otus*	*flammeolus*	NM8318	**6**	NM	Oso Ridge, 16 mi WSW of Grants	
**Otus*	*flammeolus*	NM8436	**6**	NM	Oso Ridge, 16 mi WSW of Grants	
**Otus*	*flammeolus*	NM0564	**6**	NM	Oso Ridge, 16 mi WSW of Grants	
**Otus*	*flammeolus*	NM0598	**6**	NM	Oso Ridge, 16 mi WSW of Grants	
**Otus*	*flammeolus*	NM0543	**6**	NM	Oso Ridge, 16 mi WSW of Grants	
**Otus*	*flammeolus*	NM0572	**6**	NM	Oso Ridge, 16 mi WSW of Grants	
**Otus*	*flammeolus*	NM0587	**6**	NM	Oso Ridge, 16 mi WSW of Grants	
**Otus*	*flammeolus*	NM8378	**8**	NM	Oso Ridge, 16 mi WSW of Grants	
**Otus*	*flammeolus*	NM0570	**8**	NM	Oso Ridge, 16 mi WSW of Grants	
**Otus*	*flammeolus*	NM0581	**22**	NM	Oso Ridge, 16 mi WSW of Grants	
**Otus*	*flammeolus*	NM0582	**23**	NM	Oso Ridge, 16 mi WSW of Grants	
**Otus*	*flammeolus*	NM0590	**24**	NM	Oso Ridge, 16 mi WSW of Grants	
**Otus*	*flammeolus*	NM0597	**25**	NM	Oso Ridge, 16 mi WSW of Grants	
**Otus*	*flammeolus*	NM0524	**8**	NM	Big Pigeon, San Mateo Mtns.	
**Otus*	*flammeolus*	NM0525	**27**	NM	Big Pigeon, San Mateo Mtns.	
Otus	*flammeolus*	1603-03042	**24**	NM	Scott Able Rd, 16 mi S of Cloudcroft	32˚43.382N/105˚42.895W
Otus	*flammeolus*	1603-03043	**6**	NM	Agua Chiquita Rd, 16 mi S of Cloudcroft	32˚43.496N/105˚42.056W
Otus	*flammeolus*	1603-03044	**5**	NM	Agua Chiquita Rd, 16 mi S of Cloudcroft	32˚43.277N/105˚41.794W

Genus	Species	Band/Tissue #	H	State	Specific Locality	Lat Long
Otus	*flammeolus*	1603-03045	**6**	NM	Jim Lewis Rd, 18.1 mi S of Cloudcroft	32˚42.355N/105˚38.360W
Otus	*flammeolus*	1603-03046	**2**	NM	Jim Lewis Rd, 19.2 mi S of Cloudcroft	32˚42.111N/105˚35.917W
Otus	*flammeolus*	1603-03047	**2**	NM	Wills Cyn Rd, 9.6 mi S of Cloudcroft	32˚48.912N/105˚43.264W
Otus	*flammeolus*	1603-03048	**26**	NM	Jim Lewis Rd, 17.8 mi S of Cloudcroft	32˚42.331N/105˚39.334W
Otus	*flammeolus*	1603-03049	**6**	NM	Sacramento Rd, 14.5 mi S of Cloudcroft	32˚44.756N/105˚46.490W
Otus	*flammeolus*	1603-03050	**6**	NM	Sacramento Rd, 14.8 mi S of Cloudcroft	32˚44.472N/105˚46.317W
Otus	*flammeolus*	1603-03051	**8**	NM	Sacramento Rd, 14.8 mi S of Cloudcroft	32˚44.472N/105˚46.317W
Otus	*flammeolus*	NVSE001	**6**	NV	Seligman Canyon, 28 mi SE of Eureka	39˚15.160N/115˚32.949W
Otus	*flammeolus*	NVSE002	**5**	NV	Seligman Canyon, 28 mi SE of Eureka	39˚15.407N/115˚33.070W
Otus	*flammeolus*	NVSE003	**6**	NV	Seligman Canyon, 28 mi SE of Eureka	39˚15.546N/115˚33.116W
Otus	*flammeolus*	MM032	**5**	NV	Seligman Canyon, 28 mi SE of Eureka	39˚15.546N/115˚33.116W
Otus	*flammeolus*	NVS001	**2**	NV	Seligman Canyon, 28 mi SE of Eureka	39˚15.500N/115˚33.100W
Otus	*flammeolus*	1603-03057	**28**	NV	Sagehen Canyon, 8.3 mi E of Ely	39˚16.119N/114˚43.296W
Otus	*flammeolus*	1603-03058	**8**	NV	Kalamazoo Cyn, 12.8 mi NE of McGill	39˚33.146N/114˚37.953W
Otus	*flammeolus*	1603-03059	**2**	NV	Deadman Canyon, 21 mi N of Baker	39˚18.892N/114˚10.522W
Otus	*flammeolus*	MM200	**5**	NV	Deadman Canyon, 21 mi N of Baker	39˚18.828N/114˚10.411W
Otus	*flammeolus*	DHB5807	**6**	NV	Deadman Canyon, 21 mi N of Baker	39˚18.946N/114˚10.705W
Otus	*flammeolus*	1603-03060	**5**	NV	McEllen Canyon, 30 mi SE of Eureka	39˚14.655N/115˚31.352W
Otus	*flammeolus*	JMD510	**6**	NV	McEllen Canyon, 30 mi SE of Eureka	39˚14.569N/115˚31.568W
Otus	*flammeolus*	1603-03066	**5**	NV	Berry Creek, 9.2 mi ESE of McGill	39˚19.960N/114˚38.178W
Otus	*flammeolus*	DHB5784	**5**	NV	Scofield Canyon, 9.2 mi ESE of McGill	39˚19.960N/114˚38.178W
Otus	*flammeolus*	1603-03056	**23**	NV	Canyon Creek, 11.5 mi E of Jarbidge	41˚51.663N/115˚12.439W
Otus	*flammeolus*	MM195	**2**	NV	Jim Bob Canyon, 8.9 mi E of Jarbidge	41˚52.945N/115˚15.847W
Otus	*flammeolus*	DHB5443	**6**	NV	Bear Creek Meadow, 3 mi S of Jarbidge	41˚50.140N/115˚27.141W
Otus	*flammeolus*	MM065	**6**	NV	Bear Creek Mead., 4.8 mi S of Jarbidge	41˚49.746N/115˚27.582W
Otus	*flammeolus*	NVJA01	**6**	NV	Coon Pass, 6.1 mi WSW of Jarbidge	41˚47.731N/115˚29.231W
Otus	*flammeolus*	NVJA02	**5**	NV	Seventy-Six Cyn, 10 mi S of Jarbidge	41˚44.330N/115˚28.691W
Otus	*flammeolus*	MM557	**6**	NV	Willow Creek, 9.3 mi S of Jarbidge	41˚43.436N/115˚25.711W
Otus	*flammeolus*	MM558	**5**	NV	Seventy-Six Cyn, 9 mi S of Jarbidge	41˚43.419N/115˚27.197W
Otus	*flammeolus*	1603-03063	**6**	NV	Bull Run Mtns, 12 mi SSW of Mtn. City	41˚40.344N/116˚03.819W
Otus	*flammeolus*	1603-03064	**6**	NV	Seventy-Six Cyn, 9.2 mi S of Jarbidge	41˚45.058N/115˚28.611W
Otus	*flammeolus*	1603-03065	**6**	NV	Camp Draw, 9.3 mi S of Jarbidge	41˚45.199N/115˚26.383W

Genus	Species	Band/Tissue #	H	State	Specific Locality	Lat Long
Otus	*flammeolus*	MM621	**17**	NL	Cerro Potosi, 2.7 mi W of Galeana	24˚53.287N/100˚13.575W
Otus	*flammeolus*	MM665	**17**	NL	Cerro Potosi, 2.7 mi W of Galeana	24˚53.287N/100˚13.575W
Otus	*flammeolus*	MM666	**17**	NL	Cerro Potosi, 2.5 mi W of Galeana	24˚53.133N/100˚13.309W
Otus	*flammeolus*	MM667	**20**	NL	Cerro Potosi, 2.9 mi W of Galeana	24˚53.338N/100˚13.806W
Otus	*flammeolus*	MM657	**18**	NL	Cerro Potosi, 2.6 mi W of Galeana	24˚53.223N/100˚13.425W
Otus	*flammeolus*	MM670	**19**	Coa	La Ciruela, 3.5 mi E of Monterreal	25˚13.057N/100˚23.063W
Otus	*flammeolus*	MM707	**6**	NL	Peña Nevada, 9 mi NNE of San Antonio	23˚50.415N/99˚53.762W
Otus	*flammeolus*	MM708	**17**	NL	Peña Nevada, 9 mi NNE of San Antonio	23˚50.415N/99˚53.762W
Otus	*flammeolus*	MM709	**17**	NL	Peña Nevada, 9 mi NNE of San Antonio	23˚50.183N/99˚53.746W
Otus	*flammeolus*	MM742	**21**	NL	Peña Nevada, 9 mi NNE of San Antonio	23˚50.171N/99˚53.839W
Otus	*flammeolus*	MM753	**17**	NL	Peña Nevada, 9 mi NNE of San Antonio	23˚50.444N/99˚53.796W
Otus	*flammeolus*	1603-03023	**6**	OR	Starkey Forest, 12.5 mi SW of Kamela	45˚17.376N/118˚33.187W
Otus	*flammeolus*	1603-03024	**6**	OR	Starkey Forest, 14.5 mi SW of Kamela	45˚15.287N/118˚33.297W
Otus	*flammeolus*	1603-03025	**25**	OR	Starkey Forest, 14.5 mi SW of Kamela	45˚15.287N/118˚33.297W
Otus	*flammeolus*	1603-03026	**6**	OR	Starkey Forest, 16.5 mi SW of Kamela	45˚13.558N/118˚33.952W
Otus	*flammeolus*	1603-03027	**32**	OR	Starkey Forest, 16.5 mi S of Kamela	45˚12.366N/118˚32.221W
Otus	*flammeolus*	1603-03028	**7**	OR	Starkey Forest, 15.5 mi S of Kamela	45˚13.016N/118˚31.819W
Otus	*flammeolus*	1603-03029	**6**	OR	Starkey Forest, 15 mi S of Kamela	45˚13.275N/118˚31.512W
Otus	*flammeolus*	1603-03030	**5**	OR	Starkey Forest, 15 mi S of Kamela	45˚15.438N/118˚32.521W
Otus	*flammeolus*	1603-03031	**6**	OR	Wallowa-Whitman, 4 mi SW of Kamela	45˚22.421N/118˚26.886W
Otus	*flammeolus*	1603-03032	**25**	OR	Wallowa-Whitman, 3 mi SW of Kamela	45˚22.759N/118˚26.824W
Otus	*flammeolus*	1603-03001	**25**	OR	Winema NF, 6 mi N of Chiloquin	42˚40.419N/121˚53.740W
Otus	*flammeolus*	1603-03002	**6**	OR	Winema NF, 5.5 mi N of Chiloquin	42˚40.197N/121˚54.061W
Otus	*flammeolus*	1603-03003	**29**	OR	Winema NF, 5.5 mi N of Chiloquin	42˚40.197N/121˚54.061W
Otus	*flammeolus*	1603-03004	**30**	OR	Winema NF, 12 mi N of Fort Klamath	42˚53.449N/121˚56.080W
Otus	*flammeolus*	1603-03005	**31**	OR	Winema NF, 12.5 mi N of Fort Klamath	42˚53.995N/121˚57.809W
Otus	*flammeolus*	1603-03006	**2**	OR	Winema NF, 14 mi N of Fort Klamath	42˚55.219N/121˚57.278W
Otus	*flammeolus*	1603-03007	**13**	OR	Winema NF, 12.5 mi N of Fort Klamath	42˚53.846N/121˚55.480W
Otus	*flammeolus*	1603-03008	**2**	OR	Winema NF, 7 mi SW of Fort Klamath	42˚36.454N/122˚05.549W
Otus	*flammeolus*	1603-03009	**6**	OR	Winema NF, 6 mi N of Fort Klamath	42˚48.279N/121˚57.027W
Otus	*flammeolus*	1603-03010	**13**	OR	Winema NF, 6 mi N of Fort Klamath	42˚48.279N/121˚57.027W
Otus	*flammeolus*	1603-03011	**6**	OR	Deschutes NF, 9 mi W of Sisters	44˚20.985N/121˚44.686W

Genus	Species	Band/Tissue #	H	State	Specific Locality	Lat Long
Otus	*flammeolus*	1603-03012	**2**	OR	Deschutes NF, 9.5 mi W of Sisters	44˚20.498N/121˚45.224W
Otus	*flammeolus*	CAANG01	**28**	CA	Angeles NF, 17 mi NE of Pasadena	34˚20.869N/117˚56.604W
Otus	*flammeolus*	CAANG02	**2**	CA	Angeles NF, 4 mi W of Wrightwood	34˚22.316N/117˚42.098W
Otus	*flammeolus*	CASEQ03	**6**	CA	Sequoia NF, 26 mi NE of Woodlake	36˚45.873N/118˚50.052W
Otus	*flammeolus*	CASEQ04	**6**	CA	Sequoia NF, 6 mi NE of Hot Springs	35˚58.054N/118˚37.431W
Otus	*flammeolus*	CASEQ05	**13**	CA	Sequoia NF, 26.5 mi NE of Woodlake	36˚46.435N/118˚50.376W
Otus	*flammeolus*	CASEQ06	**2**	CA	Sequoia NF, 26.5 mi NE of Woodlake	36˚46.435N/118˚50.376W
Otus	*flammeolus*	CATRI07	**6**	CA	Six-Rivers NF, 14 mi SW of Wildwood	40˚18.041N/123˚17.977W
Otus	*flammeolus*	CATRI08	**6**	CA	Six-Rivers NF, 15 mi SW of Wildwood	40˚16.271N/123˚16.889W
Otus	*flammeolus*	1603-03052	**6**	NV	Cone Peak, 4.1 mi S of Verdi	39˚27.499N/119˚58.814W
Otus	*flammeolus*	1603-03061	**6**	NV	North Canyon, 1.3 mi N of Spooner Lake	39˚07.855N/119˚54.367W
Otus	*flammeolus*	1603-03067	**6**	NV	Cone Peak, 3.7 mi S of Verdi	39˚28.006N/119˚58.508W
Otus	*flammeolus*	1603-03068	**6**	NV	Logan Creek, 3 mi SSW of Spooner Pass	39˚04.284N/119˚55.200W
Otus	*flammeolus*	MM559	**8**	NV	Logan Creek, 3 mi SSW of Spooner Pass	39˚03.883N/119˚55.079W
**Otus*	*flammeolus*	1053-96343	**5**	UT	Public Grove, 6.2 mi SE of Mantua	41˚25.588N/111˚52.106W
**Otus*	*flammeolus*	1213-78457	**5**	UT	Snowbasin, 1.2 mi NW of Ski Resort	41˚13.809N/111˚52.232W
**Otus*	*flammeolus*	912-20602	**5**	UT	Snowbasin, 1.1 mi NW of Ski Resort	41˚13.747N/111˚52.114W
**Otus*	*flammeolus*	1053-96342	**6**	UT	Public Grove, 6.2 mi SE of Mantua	41˚25.804N/111˚52.268W
**Otus*	*flammeolus*	1213-78440	**6**	UT	Snowbasin, 1.2 mi NW of Ski Resort	41˚13.835N/111˚52.312W
**Otus*	*flammeolus*	912-20603	**6**	UT	Snowbasin, 1.3 mi NW of Ski Resort	41˚13.804N/111˚52.074W
**Otus*	*flammeolus*	1053-96322	**13**	UT	3-mile Canyon, 6 mi SE of Mantua	41˚26.761N/111˚51.551W
**Otus*	*flammeolus*	1173-79904	**22**	UT	Snowbasin, 1.3 mi NW of Ski Resort	41˚13.805N/111˚52.174W
**Otus*	*flammeolus*	1083-35558	**28**	UT	Black Mountain, 3.5 mi S of Mantua	41˚26.690N/111˚57.035W
**Otus*	*flammeolus*	1173-79903	**28**	UT	Snowbasin, 1.2 mi NW of Ski Resort	41˚13.747N/111˚52.114W
**Otus*	*flammeolus*	1213-78441	**33**	UT	Snowbasin, 1.1 mi NW of Ski Resort	41˚13.720N/111˚51.671W
**Otus*	*flammeolus*	1213-78488	**34**	UT	Snowbasin, 0.2 mi N of Ski Resort	41˚13.065N/111˚51.917W
Otus	*flammeolus*	1053-96323	**9**	UT	Webster Flat, 11.3 mi SE of Cedar City	37˚34.055N/112˚54.215W
Otus	*flammeolus*	1053-96324	**6**	UT	Webster Flat, 11.1 mi SE of Cedar City	37˚34.475N/112˚54.441W
Otus	*flammeolus*	1053-96325	**5**	UT	Webster Flat, 11.4 mi SE of Cedar City	37˚33.937N/112˚54.027W
Otus	*flammeolus*	1053-96326	**6**	UT	Podunk Creek, 11.6 mi ENE of Alton	37˚30.096N/112˚16.847W
Otus	*flammeolus*	1053-96327	**10**	UT	Antimony Creek, 9 mi ESE of Antimony	38˚04.631N/111˚50.262W
Otus	*flammeolus*	1053-96328	**2**	UT	Antimony Creek, 9 mi ESE of Antimony	38˚04.631N/111˚50.262W

Genus	Species	Band/Tissue #	H	State	Specific Locality	Lat Long
Otus	*flammeolus*	1053-96329	**6**	UT	Antimony Creek, 9 mi ESE of Antimony	38˚04.288N/111˚50.641W
Otus	*flammeolus*	1053-96330	**11**	UT	Antimony Creek, 9 mi ESE of Antimony	38˚04.282N/111˚50.912W
Otus	*flammeolus*	1053-96331	**8**	UT	Antimony Creek, 9 mi ESE of Antimony	38˚04.200N/111˚50.102W
Otus	*flammeolus*	1053-96332	**12**	UT	Webster Flat, 11.1 mi SE of Cedar City	37˚33.664N/112˚55.103W
Otus	*flammeolus*	1053-96333	**8**	UT	Webster Flat, 11.1 mi SE of Cedar City	37˚33.664N/112˚55.103W
Otus	*flammeolus*	1053-96334	**6**	UT	Webster Flat, 11.2 mi SE of Cedar City	37˚33.757N/112˚54.671W

* specimen not used in Chapter 2

VITA

Graduate College
University of Nevada, Las Vegas

Markus Mika

Degrees:

Bachelor of Science, Conservation Biology, 1995
Brigham Young University

Master of Science, Zoology, 2003
Brigham Young University

Publications:

Oleyar, M. D., C. D. Marti, M. Mika, 2003. Vertebrate prey in the diet of Flammulated Owls in Northern Utah. Journal of Raptor Research

Marshall, J. C., P. Buttars, T. Callahan, J. J. Dennehy , D. J. Harris, B. Lunt, M. Mika, R. Shupe, *in press*. In The Academic Job Market, Will You Be Competitive? A Case Study in Ecology and Evolutionary Biology. Israel Journal of Ecology and Evolution

Dissertation Title: Phylogeography and Landscape Genetics of the Flammulated Owl: Evolutionary History Reconstruction and Metapopulation Dynamics

Dissertation Examination Committee:

Chairperson, Brett R. Riddle, Ph. D.
Co-Chairperson, John Klicka, Ph. D.
Committee Member, Dan B. Thompson, Ph. D.
Committee Member, Marcos Pérez-Losada, Ph. D.
Graduate Faculty Representative, Stephen M. Rowland, Ph. D