

POPULATION RESPONSE TO CLIMATE CHANGE: WINTERING STRATEGY
HAS CARRYOVER EFFECTS ON THE TIMING OF NEST INITIATION
AND MATE CHOICE IN A PARTIAL MIGRANT, THE AMERICAN KESTREL
(*FALCO SPARVERIUS*)

by

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A thesis

submitted in partial fulfillment

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in a Partial Migrant, the American Kestrel (*Falco sparverius*)

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DEDICATION

This thesis is dedicated to my Grandpa Charlie and my parents for providing me with opportunities to spend my childhood outdoors catching frogs, salamanders, and butterflies; for my mom, Mary, for sharing a love of raptors and teaching me to pick myself up when things get tough; for my Dad, Greg, for teaching me to always work hard.

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ABSTRACT

The ability of a population to respond to climate change will depend on phenotypic plasticity, adaptation, or both. Bird populations have already responded to warming temperatures by shifting their distributions, adjusting migration distance and timing, and breeding earlier. A population of American kestrels (*Falco sparverius*) in southwestern Idaho has advanced its nesting by approximately 30 days, on average, in the last 30 years and this has been correlated with changes in winter climate. The mechanisms allowing for this shift, however, are not clearly understood. I investigated if assortative mating of wintering kestrels and non-wintering kestrels is accompanying this shift by monitoring kestrels in the winter and breeding seasons from 2010-2013. I asked if 1) wintering kestrels nest earlier than non-wintering kestrels, 2) wintering kestrels tend to mate with wintering kestrels and non-wintering kestrels mate with non-wintering kestrels, and 3) early breeding kestrels are genetically differentiated from late breeding kestrels. Results indicate that wintering kestrels nest earlier than non-wintering kestrels but this effect varies across years. Wintering strategy of females significantly predicted the wintering strategy of its mate, which provides evidence for assortative mating. Analysis of 6 polymorphic microsatellite loci, however, gave no evidence of genetic differentiation or genetic structure between early and late breeding kestrels. This could be because there is still mixing between the groups despite differences in phenology, or the assortative mating pattern has arisen too recently to have resulted in genetic differentiation. Overall, this study documents that there are carryover effects of

wintering strategy on the timing of nest initiation and mate pairing in American kestrels. It provides evidence for assortative mating of kestrels by wintering strategy, but this assortative mating has not lead to genetic divergence in kestrels of southwestern Idaho at this time.

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CHAPTER 1

Introduction

Climate change is affecting the timing of life cycle events in flora and fauna worldwide (Parmesan 2006). Bird populations, in particular, have shown significant responses to climate change. For some birds, wintering distributions have shifted north (La Sorte and Thompson 2007, Paprocki et al. 2014), migration distances have decreased (Visser et al. 2009, Heath et al. 2012), arrival time to breeding areas has advanced (Jonzen et al. 2006, DeLeon et al. 2011), and a greater proportion of populations stay at breeding areas year-round (van Vliet et al. 2009). Additionally, earlier laying dates have been documented for many birds (Crick and Sparks 1999, Steenhof and Peterson 2009a). These changes in phenology could have large impacts on bird populations because the timing of reproductions often has a large impact on the survival and reproduction of individuals, two important components of fitness. There is a strong seasonal decline in the fitness of breeding birds, with early breeding birds tending to be more successful than late breeding birds (Perrins 1970). Early breeders in some populations produce more eggs (Verhulst et al. 1995, Decker et al. 2012), and they raise young that are more likely to survive (Drent 2006, Gurney et al. 2012, Serra et al. 2012). Additionally, in some populations, early hatched young are more likely to recruit back into the local population (Verboven and Visser 1998, Steenhof and Heath 2013) and tend to have greater lifetime reproductive success than late hatched young (Saino et al. 2012).

Populations of migratory bird species that have not adjusted their phenology have declined (Moller et al. 2008), which suggests that the ability for populations to shift the timing of life events will be important for their long-term persistence. The mechanisms underlying shifts in phenology, however, are not well understood. Phenological shifts could be a result of phenotypic plasticity of individuals in response to changing environmental conditions or a result of adaptation over time. Assortative mating, the non-random mating of individuals with similar phenotypes or genotypes (Jiang et al. 2013), has been suggested as a mechanism for rapid population change given selection that favors one group and inbreeding is not high enough to reduce mean population fitness (Bearhop et al. 2005, Bjorklund and Rova 2012). Additionally, assortative mating can result in reproductive isolation of subpopulations and ultimately lead to genetic divergence and sympatric speciation (Dieckmann and Doebeli 1999, Devaux and Lande 2008, Bolnick and Kirtpatrick 2012).

Most assortative mating studies in ecology have focused on non-random mating by morphological phenotypic traits (Jiang et al. 2013). Recent studies, however, have begun to assess its role in the timing of life events such as breeding and migration. As climate changes, some plant populations may exhibit assortative mating by flowering time, which may contribute to a population shift in flowering time (Franks and Weis 2009). For species that migrate, climate change during winter and migration could result in differential spring arrival times of sympatric breeding birds with wintering locations that might promote assortative mating of those groups (Flockhart and Weibe 2007). Assuming migratory behavior is under genetic control, assortative mating also may contribute to the rapid evolution of migratory divides in which members of the same

breeding population migrate to different locations in the non-breeding season. If migratory divides influence arrival time to breeding areas or body conditions of individuals, an assortative mating pattern may emerge. This has been documented in sympatric European blackcaps (*Sylvia atricapilla*) that mate assortatively by wintering area because of different arrival times to the breeding area (Bearhop et al. 2005, Irwin 2009, Rolshausen et al. 2009) and may be contributing to genetic divergence in the Swainson's thrush (*Catharus ustulatus*) (Ruegg et al. 2012).

In some cases, assortative mating has resulted in detectable genetic differentiation in sympatric groups. Genetic differentiation has been documented in sympatric band-rumped storm petrels (*Oceanodroma castro*) with different breeding times (Friesen et al. 2007) and early and late hatched Eurasian kestrels (*Falco tinnunculus*) (Casagrande et al. 2006). Genetic differentiation also has been recorded in populations with different migration strategies. Resident and migrant rainbow trout (*Oncorhynchus mykiss*) are genetically differentiated in some sympatric populations (Heath et al. 2008), and the resident subspecies of American kestrel (*Falco sparverius paulus*) is genetically differentiated from populations that also contain migrants (*Falco sparverius sparverius*) (Miller et al. 2012). These studies, however, do not assess how patterns of assortative mating and genetic divergence may be impacted by climate change.

I investigated if assortative mating by wintering strategy is associated with shifts in nesting phenology and has resulted in genetic differentiation of early and late breeding American kestrels (*Falco sparverius*) in southwestern Idaho. The American kestrel is a small, cavity-nesting falcon that is widespread in the Americas but experiencing declines in some areas (Farmer and Smith 2009, Smallwood et al. 2009). Kestrels have advanced

their timing of nesting by approximately one month, on average, in the past 30 years in a southwestern Idaho population that has not experienced decline (Steenhof and Peterson 2009a). These changes in nesting phenology have been correlated with warmer winter temperatures and decreased winter precipitation but not with changes in spring temperatures suggesting that changes in the wintering ecology of kestrels may have allowed for early breeding (Steenhof and Peterson 2009a, Heath et al. 2012, Steenhoff and Heath 2013). Winter distributions of kestrels and other raptors in the western United States have shifted north since 1975 (Paprocki et al. 2014), and over the last 50 years, kestrel migration distances have decreased in the west (Heath et al. 2012). The breeding population of kestrels in southwestern Idaho are considered partial migrants because some birds stay in breeding areas during winter and others migrate south to locations such as Arizona and Mexico (Heath unpublished data).

Different wintering strategies of birds such as residency or migration may lead to differences in the timing of nest initiation ultimately resulting in patterns of assortative mating. Environmental conditions at wintering areas or the energetic costs of migration may result in differences in body conditions of birds that may lead to assortative mating of individuals based on body condition. Assortative mating by breeding time could accelerate changes in nesting phenology over time if selection favors birds that reproduce at a certain time in the season. For kestrels in southwestern Idaho, selection may favor earlier breeding birds because there is a seasonal decline in the fitness of individuals. Analysis of long-term mark and recapture data from the southwestern Idaho kestrels indicate that adult females that breed early in the season are more likely to breed again in subsequent years (Steenhof and Heath 2009). Additionally, early hatched young are

more likely to recruit into the local population (Steenhof and Heath 2013), so there may be higher post-fledging survival associated with early nesting phenology.

I tested the hypothesis that differences in resident and migratory wintering strategies have contributed to mate choice (i.e., assortative mating), a shift in nesting phenology, and genetic differentiation in American kestrels of southwestern Idaho. The following three predictions were examined using three years of observational data and a one year assessment of levels of genetic diversity and differentiation of breeding American kestrels: 1) kestrels that winter in the breeding area will nest earlier than non-wintering kestrels, 2) wintering kestrels will tend to mate with other wintering kestrels and non-wintering kestrels tend to mate with non-wintering kestrels, and 3) early breeding kestrels will be genetically differentiated from late breeding kestrels. Alternatively, there may be interbreeding of birds with different wintering strategies and nesting phenologies or assortative mating behavior may have been initiated so recently that genetic differentiation among the early and late breeding subpopulations of American kestrels has not had time to occur.

Materials and Methods

Winter Trapping

I trapped American kestrels wintering in southwestern Idaho from 15 November through 28 February in the winters of 2010-2011, 2011-2012, and 2012-2013. I selected 15 November as a winter start date because, by this date, kestrel migration has ceased through southern raptor count sites in New Mexico (Smith and Neal 2009). I stopped trapping at the end of February to ensure that trapping ended prior to the arrival of

migratory kestrels. Kestrels were trapped with a bal-chatri baited with a live mouse (Berger and Mueller 1959) in a study area contained approximately 200 nest boxes posted in agricultural and rural areas of Ada and Canyon counties southwest of Boise, Idaho. I trapped kestrels wintering within 2 km of a nest box because kestrels in this area tend to move < 2 km from the location of winter capture to a nest box (K. Steenhof, unpublished data). Upon capture, I banded kestrels with a USGS band and an anodized alpha-numeric field-readable colored leg band on the other leg. I subsequently released kestrels within 15 minutes of capture. In addition to trapping and banding unmarked kestrels, I identified previously marked individual kestrels by reading the alpha-numeric code on the bird's color band during the 2011-2012 and 2012-2013 winters.

Nest Boxes

I monitored kestrel nest boxes in the 2011, 2012, and 2013 breeding seasons. Each year, I cleaned and added sawdust to nest boxes in early March and checked nest boxes for the presence of eggs every 10 days from the end of March until no new nests were discovered. If a pair had completed laying its clutch of eggs (5-6 eggs or no additional eggs laid after 2 days), I captured and banded both adult kestrels at the nest box by plugging the entrance and manually removing the incubating bird. It is possible to capture both the male and female breeders at nest boxes because both sexes incubate the eggs. If the pair did not have a complete clutch upon nest discovery (< 5 eggs), I estimated the number of days before the clutch would be complete $[(6 - \text{number of eggs}) * 2]$, and returned after that many days to capture incubating adults. In the 2012 breeding season, I used an insulin syringe to draw < 0.5 mls of blood for DNA analysis from incubating adult kestrels. The blood was stored on ice in the field, spun in a

centrifuge to remove plasma upon return to the laboratory, and transferred into a -80°C freezer prior to DNA extraction. In the 2013 breeding season, I identified some adults that had been previously marked by reading alpha-numeric color band codes with a spotting scope from a distance of $> 35\text{m}$ from the nest box as the bird entered or exited. In all breeding seasons, I returned to the nest box 30 days after the pair had completed a clutch to check that the eggs had hatched, and I subsequently returned to band nestlings when they were approximately 23 days old. Nestlings were aged using a photographic aging guide (Griggs and Steenhof 1993). A nesting attempt was defined as an observation of at least one egg laid, and a nesting attempt was considered successful if at least one young made it to fledging age (~ 25 days old). All breeding birds that were known to re-nest were removed from subsequent statistical analyses. The procedures in this study were conducted with approval from Boise State University's Institutional Animal Care and Use Committee (protocol #006-08-007).

Nesting Phenology

I used a generalized linear mixed-effects model with a gamma distribution and an inverse link to predict laying date. Year and wintering status were fitted as fixed effects and the identity of an individual bird as a random effect. I included a term for an interaction between year and wintering strategy. Wintering strategy was defined as a categorical variable (observed in the study area in the winter prior to breeding vs. not observed in the winter prior to breeding), and year also was treated as a categorical variable. I ran separate models for male and female kestrels because there could be sex differences in carry-over effects from the winter season, and in southwestern Idaho, kestrels change mates 32% of the time when their previous mate is known to be alive and

nesting in the area (Steenhof and Peterson 2009b). Laying dates were estimated by counting backward from the number of eggs in the box upon nest discovery [day of nest discovery - (number of eggs in box upon nest discovery * 2)]. I used Wald χ^2 tests to assess the significance of fixed effects to predict laying date ($\alpha = 0.05$), and all significant fixed effects remained in the models. I used one-tailed Wilcoxon Signed Rank Tests to compare distributions for year and wintering strategy groups. All analyses were calculated using R version 3.0.1 (R Core Team 2013).

Assortative Mating

I used a generalized linear mixed-effects model with wintering strategy of the female prior to the breeding season and year as fixed effects to predict the wintering strategy of its mate to determine if assortative mating was occurring. The identity of the individual bird was fit in the model as a random effect to account for some of the variation introduced by repeated measurements of the same bird. I included observations of birds that nested in more than one year because kestrels in this population do not always mate with the same bird each year (Steenhof and Peterson 2009b). Year and wintering strategy were treated as categorical variables. I tested the significance of the fixed effects as predictors of male wintering strategy using Wald χ^2 tests ($\alpha = 0.05$), and significant terms remained in the full model.

Microsatellite DNA

I genotyped individuals using microsatellite DNA from adult kestrels breeding in 2012. I also made comparisons between early and late breeding kestrels to determine if assortative mating has contributed to genetic differentiation among these subpopulations.

I collected blood samples from 77 adult kestrels in the 2012 breeding season and genotyped these samples using 6 polymorphic microsatellite loci originally developed for peregrine falcons (*Falco peregrinus*, Nesje et al. 2000) and gyrfalcons (*Falco rusticolus*, Nesje and Roed 2000) (Table 1). Because genetic differences have been documented between early and late hatched Eurasian kestrels (Casagrande et al. 2006), I expected to see genetic differences between the earliest quartile of breeding kestrels (n = 22; laying date of 80-90 days) and the last quartile (n = 16; laying date of 107-140 days). I expected to see differences in these groups because, in the three breeding seasons of the study, 95% of wintering kestrels laid eggs prior to the 107th day of the year, and the interquartile range of laying dates of kestrels not observed in the winter was greater than the 90th day of each year.

I extracted DNA from thawed red blood cells using an EZ Blood/Cell DNA Isolation Kit V4.0 (EZ BioResearch, St. Louis, Missouri, USA) following the manufacturer's instructions. The PCR reactions (10 uL) were performed using 10X PCR buffer, 50 mM MgCl₂, 10 mg/ml BSA, 10 mM dNTPs, 10 uM forward primer (Eurofins MWG Operon, Huntsville, Alabama, USA), 10uM fluorescent labeled reverse primer (Integrated DNA Technologies, Coralville, Iowa, USA), 5u/uL Taq polymerase (Promega, Madsion, Wisconsin, USA), and 1 uL genomic DNA. Amplifications for samples using the Fp86-2, Fr34, Fp79-4, Fp31, and Fp107 loci followed a thermal cycling protocol that included an initial denature step of 94 °C for 2 min followed by 30 cycles of the following: 94 °C for 15 s (denature), annealing temperature (Table 1) for 15 s, and 72 °C for 15 s (extension). The Fp89 locus followed a thermal cycler protocol with an initial denature step of 94 °C for 3 min followed by 30 cycles of the following: 94 °C

for 45 s (denature), 54 °C for 30 s (annealing), and 72 °C for 45 s (extension), and PCR was concluded with a final extension step of 30 min at 72 °C. Electrophoresis was conducted using a 4300 LI-COR DNA Sequencer, and I genotyped individuals by scoring alleles using Saga^{GT} Software (LI-COR, Lincoln, Nebraska, USA).

Genetic Diversity

I used MICROCHECKER Version 2.2.3 (van Oosterhout et al. 2006) to screen each locus for the presence of null alleles. Subsequently, I used Arlequin Version 3.5.1.3 (Excoffier and Lischer 2010) to calculate observed and expected heterozygosity. I used GENEPOP Version 4.2.1 (Rousset 2008) to address deviations from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium of loci: I used the recommended GENEPOP Markov Chain parameters: a dememorization of 10000 with 20 batches and 5000 iterations per batch. FSTAT Version 2.9.3.2 (Goudet 2001) was used to calculate inbreeding coefficients (F_{IS}) and the HIERFSTAT package (Goudet 2005) in R to calculate allelic richness (A_r) rarefied by the smallest subpopulation sample size.

Genetic Differentiation

I used freeNA (Chapuis and Estoup 2007) to generate F_{ST} values that were corrected for null alleles using the ENA (excluding null alleles) method which is considered to be more accurate than the INA method (including null alleles) (Chapuis and Estoup 2007) to determine the extent of genetic differentiation between early and late breeding kestrels. GENEPOP also was used to run Fisher's Exact Tests that generate P -values for genetic differentiation. Additionally, I conducted an Analysis of Molecular

Variance (AMOVA) in Arlequin to quantify genetic variation between individuals within groups and between the groups of early and late breeders.

Genetic Structure

I used STRUCTURE Version 2.3.4 (Pritchard et al. 2000) assuming an admixture model with correlated allele frequencies to address how alleles are partitioned between the four quartiles of breeding kestrels (Falush et al. 2003). The program was run with 100,000 burn-in steps with 100,000 repeats and 3 replicates for each K (1-10). I used STRUCTURE HARVESTER (Earl and vonHoldt 2012) to visualize the Ln likelihood output from STRUCTURE and to calculate ΔK , which has been suggested as the most accurate way to estimate K (Evanno et al. 2005). CLUMPP Version 1.1.2 (Jakobsson and Rosenberg 2007) was used to create a consensus among the replicates from the group with the highest ΔK , and I used DISTRUCT Version 1.1 (Rosenberg 2004) to visualize the consensus diagram of genetic structure.

Repeatability of Laying Dates

I compared laying dates for individual birds encountered as breeders in more than one year since 2008 to determine if individual kestrels nest at the same time each year. I used a linear mixed-effects model with the individual bird and year as random effects to predict laying date. I used the natural log of the laying date as the response variable to meet model assumptions, and year was treated as a categorical variable. I also used restricted maximum likelihood (REML) to obtain variance estimates for model parameters. The significance of random effects was assessed using a likelihood ratio test, and I subsequently removed year as a random effect because it was not informative ($\alpha =$

0.05). I ran models separately for male and female birds because males and females could respond differently to breeding cues or could have different physiological requirements for reproduction. I calculated repeatability estimates using the LMM.REML method following Nakagawa and Schielzeth (2010) and calculated the associated standard errors using a parametric bootstrap with 5000 permutations. All repeatability calculations were performed in the R package rptR. Significance of the repeatability of laying date for male and female kestrels was determined using a restricted likelihood ratio test on the random effect of the individual bird ($\alpha = 0.05$).

Results

I trapped 414 individual kestrels (female $n = 223$, male $n = 191$) wintering in the study area in the three years of the study. Some kestrels were observed wintering in the study area in multiple years (female $n = 19$, male $n = 18$). Most wintering birds that were already marked had been captured as adults in nest boxes. I did, however, observe kestrels wintering in the area that had been banded as nestlings in the previous breeding season (female $n = 3$, male $n = 3$), and an additional 3 birds (female $n = 1$, male $n = 2$) banded as nestlings in the 2012 season were recovered dead the following winter. One female banded as a nestling in 2012 showed long-distance movement and was found dead in Arizona in the 2012-2013 winter. The 2012-2013 winter was the coldest of the three, and during this time, a total of 16 kestrels (female $n = 9$, male $n = 7$) were discovered dead in the study area.

I documented 141 total kestrel nesting attempts, and I captured 237 kestrels (female $n = 130$, male $n = 107$) at nest boxes in the three years of the study. Some individuals were captured as breeders in more than one year (female $n = 13$, male $n = 14$).

During the study, the mean number of eggs laid per nest was 4.759 ± 0.970 with the most nests having 5 eggs. Pairs successfully fledged at least one young in approximately 50-60% of nesting attempts (2011: 51.1%, 2012: 57.4%, 2013: 59.2%). For all nesting attempts, the mean number of eggs hatched was 2.743 ± 2.236 , and the mean number of young fledged was 2.206 ± 2.163 . Of pairs that fledged at least one young, the mean number of eggs hatched was 4.430 ± 0.929 , and the mean number fledged 3.937 ± 1.223 . These measures of productivity are similar to those observed in previous seasons (Steenhof and Peterson 2009a). Of the total captures of breeding kestrels, 21 females (16.2%) and 19 males (17.8%) were observed in the study area the previous winter. Only one of 6 kestrels banded as nestlings and observed in the study area during winter subsequently nested in a box; this bird was a female hatched in 2012 and encountered as a breeder in 2013.

Nesting Phenology

I analyzed data from 210 individual birds (female $n = 117$, male $n = 93$) with known nest initiation dates in 2011, 2012, and 2013 to address differences in nesting phenology between wintering kestrels and kestrels not observed in the winter. A model with the fixed effects of year, strategy for previous winter, and a year and strategy for previous winter interaction with a random effect of individual explained laying date for both male and female kestrels (Table 2 a and b). Birds observed in the winter prior to the breeding season tended to nest earlier than birds not observed wintering in the study area, but this effect depended on year for both male and female kestrels (Fig. 2). Wintering kestrels had earlier laying dates than birds not observed in the winters of 2011 (Wilcoxon, females $W = 28.5$, $P = 0.026$; males $W = 54.5$, $P = 0.00306$) and 2013

(females $W = 61$, $P = 0.03182$; males $W = 31.5$, $P = 0.0433$); however, in 2012, laying dates of wintering kestrels and kestrels not observed in the winter did not differ significantly (females $W = 123$, $P = 0.2587$; males $W = 31.5$, $P = 0.228$).

Assortative Mating

I analyzed data from all nesting pairs in which the identity of both adults were confirmed at the nest box (breeding pairs $n = 104$, individuals $n = 208$) in the 2011, 2012, and 2013 breeding seasons. During the three years, I encountered 6 pairs of wintering birds, 22 pairs of a wintering kestrel paired with a kestrel not confirmed as wintering in the study area, and 76 pairs of non-wintering kestrels. The model with the fixed effects of female wintering strategy and year and the random effect of the identity of the female bird best predicted the wintering strategy of the female's mate. Wintering strategy of the female bird was a significant predictor of the wintering strategy of its mate (Wald $\chi^2 = 6.8689$, $df = 1$, $P = 0.008771$). Additionally, the fixed effect of year was a significant predictor (Wald $\chi^2 = 7.8865$, $df = 2$, $P = 0.019385$).

Genetic Diversity

I found evidence of null alleles at 2 of the 6 loci (Fp89 and Fr34). Null allele frequency estimates from freeNA were 0.19276 for the Fp89 locus and 0.09095 for the Fr34 locus. These frequencies are low to moderate (Chapuis and Estoup 2007). I detected no linkage disequilibrium between loci on all genotyped birds. However, there was evidence of linkage disequilibrium between the Fp31 and Fp86-2 loci for the first quartile of birds ($P = 0.0289$). Observed and expected heterozygosity was high for both early and late breeding kestrels (Table 3) compared to levels observed in other American

kestrel populations (Miller et al. 2012). For all sampled birds, all loci showed significant deviation from HWE except for the Fp86-2 locus. Three loci showed evidence for deviation from HWE for the early breeding birds, whereas only one locus showed significant deviation from HWE in late breeding kestrels (Table 3). In general, inbreeding levels as measured by the F_{IS} inbreeding coefficient were low, but inbreeding coefficients were high for the Fp89 and Fr34 loci and probably the result of null alleles at those loci (Table 3). Mean F_{IS} estimates were higher for late breeders (0.096) than early breeders (0.084), but both were lower than the inbreeding coefficients observed overall (0.116). F_{IS} were influenced by the loci in which null alleles were detected. Allelic richness (A_r) was similar across loci for early and late breeding birds and all breeding kestrels (Table 3).

Genetic Differentiation

F_{ST} values corrected for null alleles using freeNA and the ENA method were -0.010398 (95% CI = -0.013694 to -0.007437) and -0.011616 (95% CI = -0.015438 to -0.008223) in the analysis that did not correct for null alleles (the INA method). Both the ENA and INA F_{ST} analyses show similar estimates of low genetic differentiation among these two breeding subpopulations. These results suggest that the frequencies of null alleles estimated by freeNA did not have a large effect on the estimates of genetic differentiation. Fisher's exact tests showed no significant genetic differentiation between early and late breeding kestrels ($\chi^2 = 6.04771$, $df = 12$, $P = 0.913658$, $\alpha = 0.05$). AMOVA showed similar results (Table 4). Almost all genetic variance was explained by variance within individuals (93.95%) and among individuals within groups (7.15%) instead of between early and late breeding subpopulations (-1.10%).

Genetic Structure

There was no evidence of genetic structure across the quartiles of breeding kestrels. Results from STRUCTURE HARVESTER showed that $K = 1$ group had the highest Ln likelihood (-1635.4, Fig. 3), suggesting that genetic diversity was equally partitioned between early and late breeding American kestrels in this population. The ΔK analysis suggested that 3 allele groups were the most likely genetic structure (Fig. 3), but visualization of the data confirmed a lack of genetic structure by breeding time (Fig. 4).

Repeatability of Laying Date

I analyzed data from 44 adult kestrels that nested in the study area in more than one year since 2008 (female $n = 23$, male $n = 21$). Most females were sampled in only two years ($n = 20$), but 3 individuals were sampled in more than two years. Males were more likely to be captured in more than 2 breeding seasons ($n = 8$). Females had lower repeatability of laying dates ($R = 0.075$, S.E. = 0.126, 95% C.I.: 0-0.410, $P = 0.3112$). Males, however, were more repeatable in the timing of nest initiation ($R = 0.373$, S.E. = 0.155, 95% C.I.: 0.017-0.637), and this relationship was significant ($P = 0.0154$).

Discussion

I found that wintering kestrels initiated nesting earlier than kestrels not observed in the winter, but this relationship depended on year; wintering kestrels did not nest significantly earlier than non-wintering kestrels in 2012. Female kestrels that bred in the study area in multiple years did not consistently lay eggs at the same time each year, but timing of nest initiation by males was more repeatable across years. Additionally, the wintering strategy of females was a significant predictor of the wintering strategy of its

mate, providing evidence for assortative mating. Although I documented differences in phenology of wintering and non-wintering kestrels and evidence of assortative mating of kestrels by wintering strategy, I did not detect significant genetic differentiation or structure between early and late nesting kestrels.

Earlier nest initiation of kestrels that wintered in the breeding area in 2010-2011 and 2012-2013 is consistent with historical observations from this population (Steenhof and Peterson 2009a) and has also been documented in other breeding populations of American kestrels in the Pacific Northwest (Henny and Brady 1994). Earlier breeding of winter resident birds compared to migrants also has been documented in other partial migrant populations including populations of snowy plovers (*Charadrius alexandrinus*) (Warriner et al. 1986) and American dippers (*Cinclus mexicanus*) (Morrissey 2004). Because we did not determine arrival time of migrants to breeding areas, we could not clarify if differences in nesting phenology between wintering and non-wintering birds were a result of differences in arrival time to breeding areas or of carryover differences from the wintering strategies such as body condition.

Although I found differences in nesting phenology of wintering and non-wintering birds in two years, I did not find differences in the nesting phenology in 2012, and this could be a result of kestrels changing wintering strategies with different winter conditions. Migratory tendency is influenced by both genetic variation and environmental conditions (Ogonowski and Conway 2009, Pulido 2011). Although a gene associated with migratory tendency has been discovered (Mueller et al. 2011), most studies of partial migration suggest that migratory tendency is condition-dependent (Chapman et al. 2011). Condition-dependent migratory tendency can be explained by the

environmental threshold model of partial migration (Pulido 2011, Supplemental Fig. 3), which states that partial migrant populations consist of obligate residents and obligate migrants as well as facultative migrants that change migratory tendency depending on environmental conditions. Studies have shown that birds can change migratory tendency over their lifetimes, particularly changing from migrants to residents with age. Individual lesser black-backed gulls (*Larus fuscus*) migrate shorter distances as they get older (Marques et al. 2010), and western burrowing owls (*Athene cunicularia hypugaea*) tend to transition from migrants to residents as they age (Ogonowski and Conway 2009). Some populations, however, such as great bustards (*Otis tarda*) breeding in central Spain may change their migratory tendency regardless of age (Palacin et al. 2011).

If American kestrels show similar patterns of facultative migration in a portion of the population, facultative migrants may nest earlier in years following winter residency compared to years in which they migrated out of the breeding area. In the study, some kestrels may have changed wintering strategies in the 2011-2012 winter because it was warmer and drier than the other years of the study. Of the three winters, the 2011-2012 winter in the southwestern Idaho valleys was warmest (~1.1°C warmer, highest average temperature anomaly) and driest (0.89-2.52 cm less precipitation, lowest average precipitation anomaly) from November through February (NOAA National Climatic Data Center, Supplemental Table 1 and 2; Supplemental Fig. 1 & 2), and no difference in nesting phenology was documented between wintering and non-wintering kestrels in the subsequent breeding season. In this year, a greater portion of kestrels may have stayed as residents and subsequently nested earlier compared to other years. Additionally, kestrels may have migrated shorter distances in the warm winter compared to colder winter

seasons, which could lead to earlier arrival to the breeding areas. This is supported by results from Heath et al. (2012) who found that kestrel migration distances in the western United States decrease in warmer winters.

Facultative migrants may stay as residents in mild winters because warm winters might remove thermoregulatory constraints (Ketterson and Nolan 1976, Belthoff and Gauthreaux 1991) or increase availability of food resources, which could decrease competition between individuals (Gauthreaux 1982, Brodersen et al. 2008). When conditions are harsh at breeding areas in the winter, there may be a trade-off between the advantages of early breeding associated with residency and increased survival associated with migration (Whitehorne 2010). Finally, it is possible that I observed no difference in 2012 because we did not catch a high enough proportion of wintering kestrels to detect a difference between the wintering and non-wintering groups compared to the other years of the study.

The ability of assortative mating to result in changes of subsequent generations depends on the strength and consistency of the assortative mating and the extent the phenotype is under genetic control. If wintering strategy is condition-dependent for a portion of the southwestern Idaho kestrel population, assortative mating may not have a large effect on shifts in nesting phenology because patterns may not be consistent each year. Additionally, this study showed that the phenotype of laying date is not always repeatable and may have stronger environmental controls than other phenotypic traits which could limit assortative mating effects on future generations. A review study by Jiang et al. (2013) showed that the strength of assortative mating, as measured by correlation of traits of female and male mates, varies by taxa, and in birds, assortative

mating strength tends to be low compared to fish and crustaceans but similar to levels observed in insects and amphibians. Almost all of these studies, however, investigate the strength of assortative mating by size and structural characteristics, not phenology or behavior, and the strength of assortative mating by those traits may be higher than assortative mating by morphometric traits. Although sample size was small, Jiang et al. (2013) found some evidence that assortative mating by phenology may be stronger than other types of assortative mating, which could suggest that assortative mating by breeding time may facilitate population change a greater rate than other forms of assortative mating.

Patterns of assortative mating in this population may not be consistent enough to eliminate or restrict gene flow between early and late breeding kestrels. In addition to mixing after warm winters, interbreeding of the groups could occur if birds re-nest with individuals with a different wintering strategy. American kestrels in southwestern Idaho may re-nest if their first nest attempt fails, and they do not always nest with the same mate even when that bird is known to be alive (Steenhof and Peterson 2009b). Additionally, in some years, early breeding kestrels may produce two broods (Steenhof and Peterson 2009a), and this also could lead to gene flow if double-brooding adults mate with a bird with a different wintering strategy. It also is possible that early breeding male kestrels who have already nested may copulate with late breeding females who are bonded with another male resulting in extra-pair paternity, and this could contribute to mixing of birds with different wintering strategies. Levels of extra pair paternity have not been investigated in the southwestern Idaho breeding population of kestrels, but

Villarroel et al. (1998) found evidence of extra pair fertilities in 10% of American kestrel nests in a Quebec population.

Gene flow between the groups could result from plasticity in timing of reproduction. The repeatability analysis suggests that female kestrels are less consistent in the timing of reproduction each year than males. Although the confidence intervals for the analysis are large, the results are consistent with previous studies that have observed males to have more repeatable behavior than females (Bell et al. 2009). Behaviors may be less repeatable for females long-term because poorly timed egg production may have greater fitness costs for females than males. This could be because egg production requires high energy and nutrient investment and may result in suppressed immune function (Williams 2005). Additionally, male and female birds may respond differently to cues regulating reproduction (Ball and Ketterson 2008). For example, males may primarily respond to photoperiod cues, but females may integrate more supplemental cues such as climate conditions, resource availability, or behavioral cues from mates to adjust reproductive timing. The non-repeatability of females in laying dates across years may contribute to random mating. However, laying date may be more repeatable in female kestrels than our data indicate because most female kestrels were detected breeding for only two years.

Despite evidence for assortative mating by wintering strategy in this breeding population, I did not observe genetic differentiation in early and late breeding kestrels or genetic structure by breeding time. Assortative mating should increase homozygosity without changing allele frequencies in populations (Crow and Felsenstein 1968) if the phenotypic trait is under genetic control, but I observed high levels of heterozygosity

across all loci compared to Miller et al. (2012) who also used microsatellite DNA to investigate genetic diversity and differentiation between American kestrels populations in the western and eastern United States. Additionally, I would expect to see evidence of inbreeding across all loci in the late and early breeding groups, but inbreeding coefficient levels were influenced primarily by loci showing evidence of null alleles. Overall, results from the microsatellite analyses support panmixia between kestrels in southwestern Idaho. This result agrees with Miller et al. (2012) who found kestrels from southwestern Idaho to be part of a larger western United States breeding population. Miller et al. (2012) did find, however, that the non-migratory subspecies of American kestrel (*Falco sparverius paulus*) was genetically different from other eastern populations that contain migrants. Also, our results do not agree with Casagrande et al. (2006) who found significant genetic differences between early and late breeding Eurasian kestrels. This could be because changes in wintering behavior and nesting phenology in southwestern Idaho may have not occurred long ago enough for divergence to occur between early and late breeders.

Overall, this study suggests that wintering strategy of individuals can have carryover effects on mate selection and the timing of reproductive activity of American kestrels. Results indicate that kestrels wintering in southwestern Idaho nest earlier than non-wintering kestrels in some years, and kestrels tend to mate assortatively by wintering strategy. At the time of the study, however, the assortative mating pattern has not resulted in genetic differentiation or structure of kestrels by breeding time, which suggests this is a panmictic population. Shifts in nesting phenology observed in kestrels of southwestern Idaho over 30 years may be associated with these assortative mating

patterns, but assortative mating may not be consistent or recent enough to result in genetic divergence. The trend towards earlier nesting phenology in this population may be a result of plasticity of individuals in migratory tendency and reproductive timing of associated with changing environmental conditions. Additional research will be needed to elucidate the mechanisms underlying nesting phenology shifts in American kestrels of southwestern Idaho because improperly timed reproductive attempts may reduce mean population fitness.

Tables

Table 1. Characteristics of 6 polymorphic microsatellite loci screened for American kestrels in this study including GenBank accession number from original source, fluorescent label, primer sequence, repeat motif, annealing temperature (T_A), and number of alleles observed for each locus on all genotyped individuals (n = 77).

locus	source	GenBank accession no.	fluorescent label	primer sequence 5'-3'	repeat motif	T_A	total no. of alleles
Fp86-2	Nesje et al. 2000	AF118429	700	F: GTAAATAAGCCTCCAAAAGG R: CATGCTTCCTGATTACTTC	(CA) ₁₁	56	8
Fr34	Nesje and Roed 2000	AF200200	700	F: TATTTTCAGCCTGGTTTCCTAT R: TTTAGTATCTCAAAGACCCTGTGT	(GT) ₉	56	16
Fp79-4	Nesje et al. 2000	AF118427	700	F: TGGCTTCTCTTATCAGTAAC R: GGCTGGGTGGAATTAAAG	(CA) ₁₆	56	35
Fp31	Nesje et al. 2000	AF118422	800	F: ATCACCTGCACATAGCTG R: TTTAGCTCCTCTCTCTCAC	(CA) ₁₇	54	10
Fp107	Nesje et al. 2000	AF118434	800	F: ACAGATTTGATTGCCAGG R: TGCCATGTCACATTCATAC	(GT) ₁₁ TT(GT) ₈	56	15
Fp89	Nesje et al. 2000	AF118430	800	F: CTCTGCCCTGAATACTTAC R: GAATCTTGTTTGCATTGGAG	(AT) ₁₂	54	6

Table 2. Analysis of nesting phenology by wintering strategy using laying dates of (a) female and (b) male American kestrels breeding in southwestern Idaho in 2011-2013. All fixed-effects were significant at $\alpha = 0.05$. Both models included a random variable of individual bird. Asterisks designate significant *P*-values.

a)			
fixed variable	Wald χ^2	<i>df</i>	<i>P</i>
year	17.414	2	0.0001654*
previous winter	0.317	1	0.5734377
year*previous winter	14.256	2	0.0008023*
b)			
fixed variable	Wald χ^2	<i>df</i>	<i>P</i>
year	6.0307	2	0.04903*
previous winter	0.3268	1	0.56754
year*previous winter	7.7226	2	0.02104*

Table 3. Observed heterozygosity (H_o), expected heterozygosity (H_e), allelic richness (A_r), and inbreeding coefficients (F_{IS}) overall and for each locus for American kestrel breeding in 2012 (total $n = 77$, early $n = 22$, late $n = 16$). Asterisks designate significant deviations from Hardy Weinberg Equilibrium at $\alpha = 0.05$.

locus	all breeding kestrels				early breeding kestrels				late breeding kestrels			
	H_o	H_e	A_r	F_{IS}	H_o	H_e	A_r	F_{IS}	H_o	H_e	A_r	F_{IS}
Fp86-2	0.66667	0.69238	4.922	0.038	0.72727	0.72939	5.669	0.003	0.68750	0.68347	3.924	-0.006
Fr34	0.72727	0.89842*	8.286	0.192	0.81818	0.88901*	8.235	0.081	0.68750	0.84476	6.569	0.191
Fp79-4	0.94000	0.96303*	12.471	0.024	0.85714	0.95122*	11.707	0.101	0.81250	0.95968 *	12.076	0.158
Fp31	0.78462	0.84293*	6.126	0.07	0.81818	0.84144	5.976	0.028	0.81250	0.85887	6.320	0.056
Fp107	0.92453	0.86453*	8.469	-0.07	0.90909	0.89852*	8.539	-0.012	0.93750	0.90726	8.625	-0.034
Fp89	0.44118	0.80465*	4.845	0.455	0.55000	0.79024	4.782	0.309	0.64286	0.79894	5.427	0.201
across loci	0.74738	0.84432	7.520	0.116	0.77998	0.84997	7.485	0.084	0.76339	0.84216	7.157	0.096

Table 4. Analysis of molecular variance (AMOVA) comparing early and late breeding American kestrels in southwestern Idaho in 2012. Analysis was conducted using F_{ST} values in Arlequin Version 3.5.1.3 (Excoffier and Lischer 2010). Significant P -values at $\alpha = 0.05$ are designated with an asterisk.

source of variation	<i>df</i>	sum of squares	variance components	percentage variation	P -value
among groups	1	1.632	-0.02674	-1.10	1.00000
among individuals within groups	36	94.420	0.17324	7.15	0.00684*
within individuals	38	86.500	2.27632	93.95	0.01369*
total	75	182.553	2.42282		

Figures

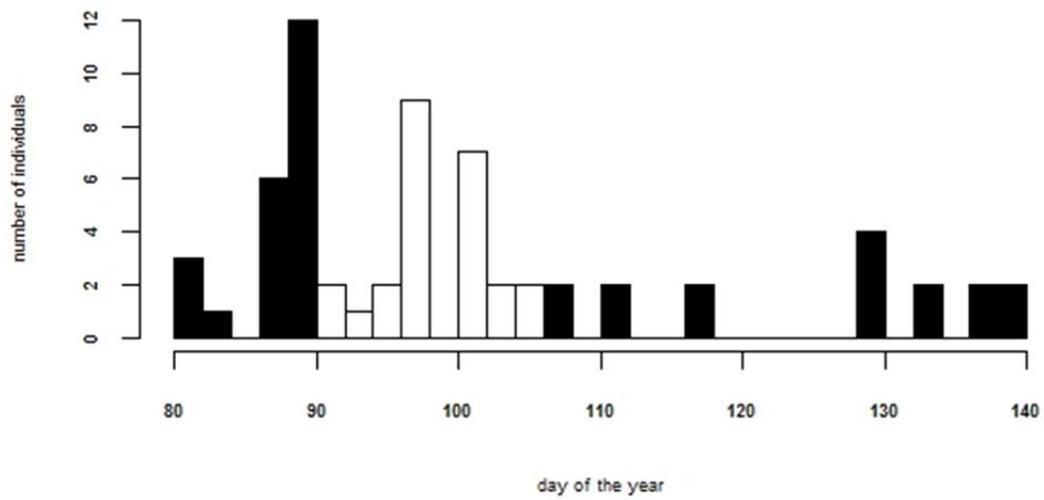


Figure 1. Distribution of laying dates from 77 American kestrels breeding in southwestern Idaho in 2012. Genetic differentiation between early and late breeding kestrels was assessed using the first quartile of breeding kestrels ($n = 22$) and last quartile of kestrels ($n = 16$) both designated in black.

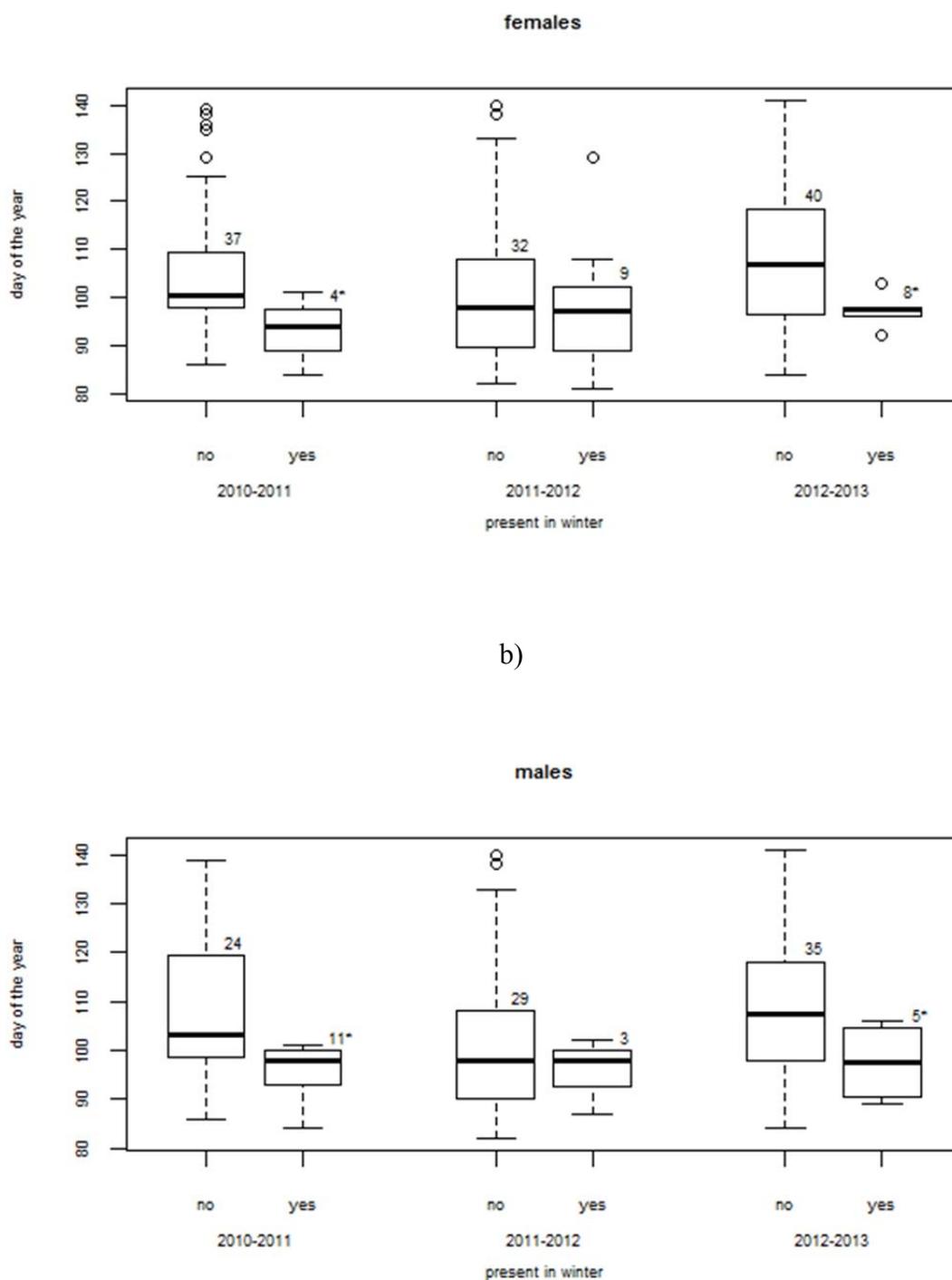


Figure 2. Boxplot of the interaction between wintering strategy (kestrel present in study area in the winter prior to breeding vs. not observed in the study area in the winter) and year in predicting laying date for of a) female kestrels and b) male kestrels. Sample sizes are listed above each box plot, and significant differences

between wintering and non-wintering American kestrels for each year are designated with an asterisk ($\alpha = 0.05$).

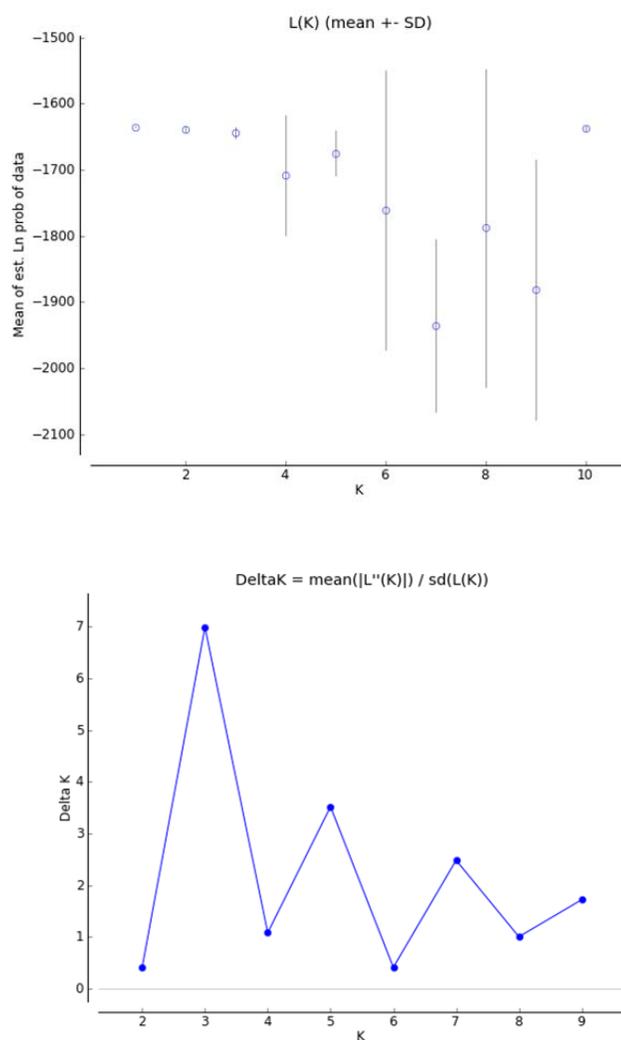


Figure 3. Natural log likelihood data from STRUCTURE HARVESTER suggest that $K = 1$ ($\text{Ln } P(D) = -1635.4$) is most likely for American kestrels breeding in southwestern Idaho. This indicates there is no genetic structure by breeding time. Results from STRUCTURE HARVESTER suggest a ΔK of 3 genetic clusters was most likely.

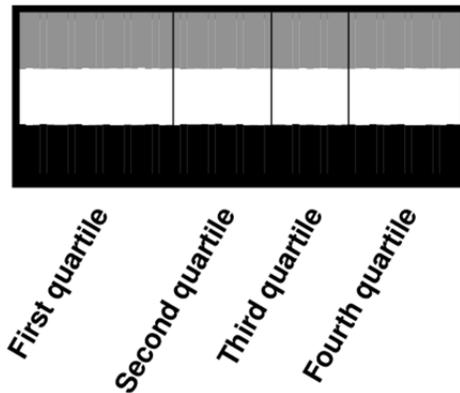


Figure 4. Barplots for STRUCTURE showing association of genetic clusters for $K = 3$. Results suggest a lack of genetic structure of American kestrels in southwestern Idaho by breeding time during the 2012 breeding season.

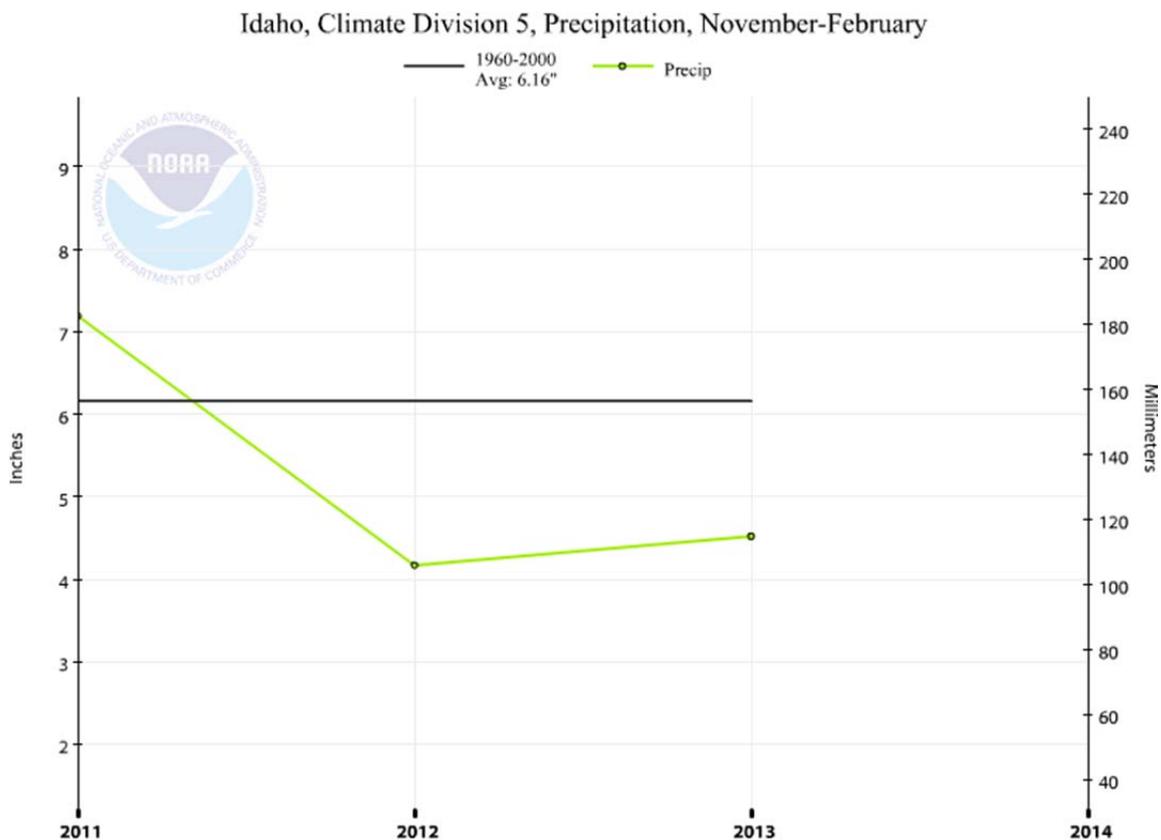
Supplemental Tables and Figures

Supplemental Table 1. November to February average precipitation anomalies in mm in the valleys of southwestern Idaho in which the study was conducted. Precipitation anomalies were calculated from a 1960-2000 base period.

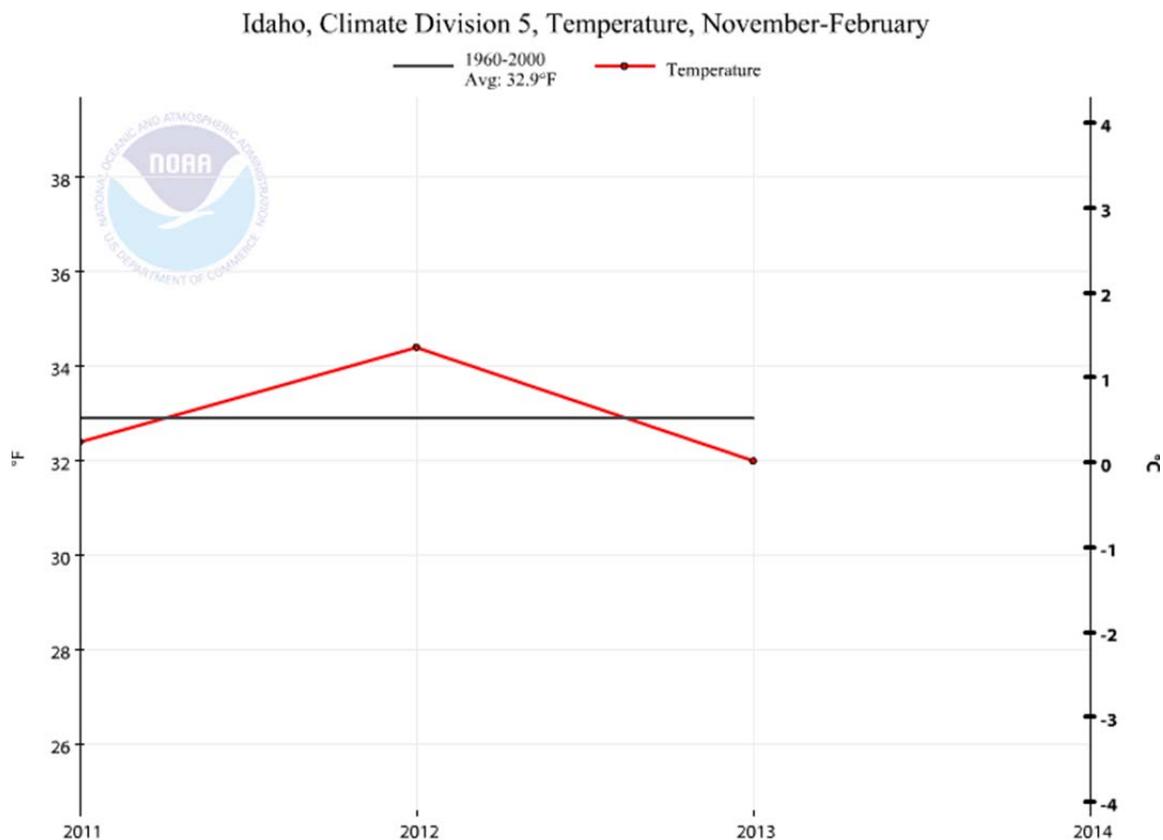
year	total	anomaly
2010-2011	182.6	26.1
2011-2012	105.9	-50.5
2012-2013	114.8	-41.7

Supplemental Table 2. November to February average temperatures anomalies in degrees Celcius in the valleys of southwestern Idaho in which the study was conducted. Temperature anomalies were calculated from a 1960-2000 base period.

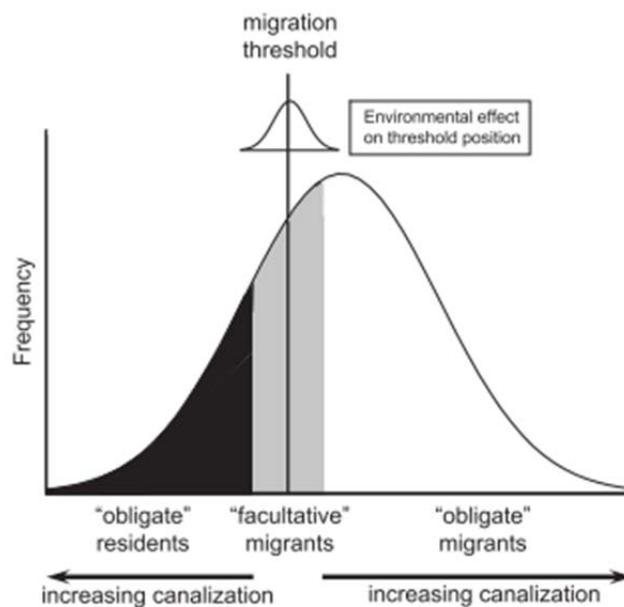
<u>year</u>	<u>average</u>	<u>anomaly</u>
2010-2011	0.22	-0.28
2011-2012	1.33	0.83
2012-2013	0.0	-0.50



Supplemental Figure 1. November to February average precipitation anomalies in inches and mm in the valleys of southwestern Idaho in which the study was conducted. Precipitation anomalies were calculated from a 1960-2000 base period.



Supplemental Figure 2. November to February average temperatures anomalies in degrees Celcius in the valleys of southwestern Idaho in which the study was conducted. Temperature anomalies were calculated from a 1960-2000 base period.



Supplemental Figure 3. Diagram of the environmental threshold model of migration from Pulido (2011) shows a hypothetical distribution of migratory tendency of a population. A proportion of individuals in the population are “obligate residents” (black) and stay at the breeding area all year, whereas “obligate migrants” (white) always migrate regardless of the year. “Facultative migrants” (grey), however, change migratory tendency depending on the environmental conditions that year resulting in more birds staying as residents in the breeding area in mild winters compared to harsh winters.

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