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Research Article

Effect of Compensatory Immigration on the Genetic Structure of Coyotes

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ABSTRACT Despite efforts to reduce their effects on livestock and native ungulates within the southeastern United States, coyotes (*Canis latrans*) can recover from control programs. It is unknown how coyotes compensate for high mortality following trapping, so there is great interest to identify methods that can provide insight into coyote response to intensive trapping. To investigate if population genetic tools can decipher how coyotes recover from intensive trapping, we combined an empirical test of how genetic differentiation, diversity, and familial structure changed following trapping on the Savannah River Site (SRS), South Carolina, USA, with spatially explicit genetic simulations. The pre- and post-trapping periods had similar genetic diversities and were not genetically differentiated as expected by either compensatory reproduction or immigration from a single genetic source. The post-trapping coyote populations exhibited weaker signatures of philopatry with little evidence for increased dispersal distances of young coyotes, which suggests immigration caused a decrease in familial structure. Our simulations indicated that spatial autocorrelation coefficients and observed heterozygosities change as immigration increases, whereas population differentiation, allelic richness, and displacement distances do not. Collectively, our results suggest that coyotes recover from intensive trapping via reproduction and immigration, which likely makes preventing compensation difficult. Monitoring post-trapping populations may offer more insight into maximizing the effectiveness of control efforts, and based on our simulations, population genetics can provide critical information about the amount of compensatory immigration following trapping.

KEY WORDS *Canis latrans*, compensatory immigration, compensatory reproduction, coyote, South Carolina, spatial autocorrelation, trapping.

Carnivores deemed overly abundant are often the subject of intense control efforts to reduce human-predator conflicts (Robinson et al. 2008, Minnie et al. 2016), boost abundance of prey species (Kilgo et al. 2012, Lazenby et al. 2014), prevent range expansion (Melero et al. 2010), or reduce disease transmission (Donnelly et al. 2003). Despite considerable effort in removing carnivores, reports on effectiveness of control programs are mixed (Donnelly et al. 2003, Robinson et al. 2008, Lazenby et al. 2014, Conner and Morris 2015, Minnie et al. 2016) with some programs reported as ineffective at controlling carnivore numbers (Bodey et al. 2011, Lazenby et al. 2014, Newsome et al. 2014). One factor that decreases the effectiveness of control efforts is cost, which often limits the spatial and temporal extents to which control programs can be conducted. Many carnivores are continuously distributed, but control efforts often occur at small spatial or temporal scales. As a result, removing a large number of individuals from a local area may cause dramatic changes in processes like dispersal and mortality compared to uncontrolled populations (Robinson et al. 2008, Gervasi et al. 2015, Minnie et al. 2016).

The ability of localized lethal control to alter population dynamics within previously continuous populations is documented in carnivores (Pope et al. 2007, Robinson et al. 2008, Gervasi et al. 2015), but how species respond to high mortality is dependent on species-specific traits like dispersal patterns, social structure, and reproductive strategies (Frank and Woodroffe 2001). For example, many mesocarnivores recover quickly from lethal control (Bodey et al. 2011, Lazenby et al. 2014, Lieury et al. 2015, Minnie et al. 2016) because of their high intrinsic growth rate (Frank and Woodroffe 2001) and plasticity in reproductive and dispersal strategies. Mesocarnivores can respond to lethal control by increasing reproductive output (i.e., larger litter sizes; Knowlton 1972, Windberg 1995; younger age at reproduction; Sterling et al. 1983, Minnie et al. 2016) or increased rates of immigration into control areas (Beasley et al. 2013, Lazenby et al. 2014, Lieury et al.

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2015, Minnie et al. 2016), which in turn can limit the temporal success of control programs. Understanding how these compensatory mechanisms (i.e., reproduction or immigration) contribute to the recovery of controlled populations, therefore, is important for maximizing the effectiveness of lethal control (Beasley et al. 2013, Lieury et al. 2015).

One species where lethal control can be difficult is the coyote (*Canis latrans*; Knowlton et al. 1999) because like many other mesocarnivores (Lazenby et al. 2014, Lieury et al. 2015, Minnie et al. 2016), coyotes often quickly recover from control efforts. For example, even with sustained intense trapping over several years in South Carolina (~75% of coyotes; Kilgo et al. 2014), white-tailed deer (*Odocoileus virginianus*) experienced limited success in recruitment because of incomplete removal of resident coyotes and rapid recovery of coyotes (Kilgo et al. 2014). Coyotes have differing dispersal and reproductive output according to population densities (Knowlton 1972, Connolly and Longhurst 1975, Sacks 2005), so it is unclear if reproduction, immigration, or both fuel recovery in coyotes. Previous research (Kilgo et al. 2017) reported evidence for younger breeding ages in coyotes in South Carolina and simulation (Connolly and Longhurst 1975, Sterling et al. 1983, Pitt et al. 2003) and empirical tests of removals in western populations (Gese 2005) suggest that compensatory reproduction and immigration can contribute to population recovery. Immigration is thought to be the primary mechanism of recovery in other mesocarnivores (Lazenby et al. 2014, Lieury et al. 2015, Minnie et al. 2016), but overall, we know very little about how coyotes recover from lethal control outside of agricultural operations (Blejwas et al. 2002).

One potential method that could elucidate how coyotes respond to lethal control is population genetics because previous studies reported changes in genetic structure due to compensatory immigration (Abdelkrim et al. 2007, Pope et al. 2007, Gervasi et al. 2015, Oliver et al. 2016). One potential outcome of compensatory immigration occurs when separate populations colonize a culled or hunted area, which results in mixing from multiple genetic sources following lethal control and an increase in genetic diversity (Abdelkrim et al. 2007). These situations typically occur on island eradications (Abdelkrim et al. 2007) or within metapopulations (Andreasen et al. 2012) where separate genetic populations colonize the culled area. Other authors have reported changes in population genetic structure based on altered dispersal regimes within a single population (Pope et al. 2007, Oliver et al. 2016). Specifically, genetic signatures of familial structure (i.e., presence of related individuals at fine spatial scales) weakened based on increased immigration into a trapped area (Oliver et al. 2016) or increased frequency of dispersal away from natal areas (Pope et al. 2007). Dispersal in mesocarnivores such as coyotes is notoriously difficult to study in the field, but changes in genetic differentiation, diversity, and familial structure could potentially help understand how species recover following lethal control.

Despite the obvious utility of population genetics in monitoring populations following lethal control, relatively few studies have been conducted with mesocarnivores (Pope et al. 2007, Oliver et al. 2016). Therefore, generating testable expectations of how genetic structure may change following lethal control can be problematic given the wide variety of potential genetic responses to lethal control. Predictions in population genetics are largely based on models that assume a relatively narrow set of conditions (e.g., equilibrium between evolutionary processes and specific mutation models). Recent demographic changes often cause deviations from these conditions (Donnelly et al. 2001), which in turn limits the applicability of established models to actual populations (Putman and Carbone 2014). Another potential pitfall for investigating changes in genetic structure following lethal control is that mesocarnivores typically exhibit weak genetic structure at local spatial scales (Dharmarajan et al. 2009, Croteau et al. 2010, Brashear et al. 2015). When genetic differentiation is weak, it can be difficult to determine if genetics methods have the power to detect subtle changes in fine-scale genetic structure, especially when studies are limited by logistical or financial constraints (e.g., limited no. samples, genetic markers, spatial scale of study). Therefore, coyotes present a difficult case to develop realistic expectations for genetic structure and determine whether statistical results can detect subtle changes in fine-scale genetic structure.

Genetic structure is the result of many interacting demographic and genetic processes that are difficult to fully understand in wild populations, but the use of simulations provides a method to model these processes and their influence on genetic structure (Hoban et al. 2012). Simulations allow control over relevant demographic and genetic processes (e.g., mutation, population size, migration rates, selection; Hoban 2014), which can then produce testable hypotheses about resultant genetic structure. With the increasing availability and diversity of simulation software, simulations have produced predictions for many questions such as the effects of bottlenecks, climate change, and translocations on genetic structure (Hoban 2014) but to date have not been applied to predicting the genetic effects of lethal control. In addition to the ability to generate appropriate hypotheses, simulations can also validate whether specific statistical techniques are appropriate for detecting changes in genetic structure (Hoban et al. 2012). Of particular importance is evaluating the effects of incomplete sampling because studies with mesocarnivores often suffer from limited spatial and temporal sampling, clumped samples, low sample sizes, and low number of genetic markers, all of which can affect statistical power to detect genetic structure (Schwartz and McKelvey 2009, Landguth et al. 2012, Oyler-McCance et al. 2013). By replicating known sample issues on simulated populations, authors can then evaluate the impact of these limitations on inferred genetic structure (Kierepka and Latch 2016). Simulations can provide invaluable insight into how lethal control and subsequent immigration influence genetic structure.

To understand how coyotes recover from intensive control measures, we focused on 3 aspects of genetic structure of coyotes before and after lethal trapping on the Savannah River Site (SRS), South Carolina, USA: population differentiation, genetic diversity, and familial structure. In addition to the empirical analysis, we evaluated how measures of population differentiation, genetic diversity, and familial structure change with increasing levels of compensatory immigration via spatially explicit simulations. These simulations also allowed us to investigate if sampling pitfalls inherent to our empirical dataset (i.e., limited no. genetic markers, unequal sample sizes between yrs) influenced our ability to detect changes in genetic structure across levels of compensatory immigration.

STUDY AREA

Contractors conducted coyote trapping on the SRS, a United States Department of Energy field office in South Carolina that is restricted to the public. The SRS encompasses 78,000 ha of predominantly forested land cover within the Upper Coastal Plain physiographic region of South Carolina (36–104 m elevation). Upland areas (~68% of SRS) on the SRS mainly contain loblolly (*Pinus taeda*) and longleaf (*P. palustris*) pines, whereas bottomland areas (22% of SRS) contain hardwoods and cypress (*Taxodium distichum*)-tupelo (*Nyssa* spp.; White and Gaines 2000, Imm and McLeod 2005). Forested areas contain a number of wildlife species including white-tailed deer (*Odocoileus virginianus*), turkey (*Melegris gallopavo*), raccoon (*Procyon lotor*), and bobcat (*Felis rufus*). The United States Forest Service manages the forested areas on SRS. In addition to forest, clear-cuts and developed areas comprise the remaining 10% of SRS. Human land use includes 20 separate SRS facilities (1,781 ha), transport infrastructure (225 km primary roads, 2,253 km secondary roads, and 96 km of railway), and scattered human facilities less than 1 ha in size (Blake et al. 2005). The SRS is characterized by a warm ($\bar{x}$ monthly temp = 15.39–33.44°C), humid ($\bar{x}$ monthly humidity = 63–80%) climate. Rainfall averages 7.11–13.92 cm/month, and soils range from sandy in the uplands to clay-loam soils in the lowlands (Rogers 1990). Coyotes were first recorded on SRS during the 1980s and estimated densities reached 0.8–1.5 coyotes/km^2 prior to trapping (Schrecengost et al. 2008). Harvest of coyotes on SRS prior to 2010 was limited to opportunistic shooting (<25 coyotes/year; Kilgo et al. 2014), but human-caused mortality was much greater outside SRS (Schrecengost et al. 2009).

METHODS

Coyote Trapping

A complete description of the trapping treatments and abundance response is available in Kilgo et al. (2014). Briefly, hired contractors trapped and killed coyotes within 3, 32-km^2 trapping areas, each separated by ≥6.4 km, from 18 January to 6 April each year from 2010–2012 (Kilgo et al. 2014). All trapping protocols adhered to South Carolina Department of Natural Resources Research Collection Permit No. 010610-01. Contractors recorded sex and mass for each animal and extracted a lower canine for aging via cementum annuli (Matson's Laboratory, Milltown, MT, USA). Contractors trapped 474 coyotes from 2010–2012 across the 3 study areas (169, 137, and 168 in 2010, 2011, and 2012, respectively). The trapping effort resulted in an estimated 75% short-term decrease in overall coyote numbers across the study area (Kilgo et al. 2014).

Although contractors trapped 474 coyotes, funding limited our ability to genotype all the individuals, so we collected tissue samples from 311 coyotes: 169, 77, and 65 from 2010, 2011, and 2012, respectively (Fig. 1). We used genetic methods for multiple projects (i.e., identifying potential depredations), so we prioritized older animals for genotyping in 2011 and 2012. We acknowledge the prioritization of adult animals may dampen the effects of compensatory immigration because immigrants are expected to be younger animals. Also, the proportion of individuals ≤1 year old within all the trapped individuals increased from 58% in 2010 to 67–73% in 2011 and 2012 (Kilgo et al. 2014), whereas age ratios for genotyped animals were 72%, 77%, and 65% animals ≤1 year old for 2010, 2011, and 2012, respectively. However, budgetary limitations are often encountered in monitoring projects, so a major goal of this study was to understand if genetics could aid in post-trapping monitoring even with limitations like reduced sample sizes.

Based on the differences in sample sizes between years and sample areas, we designated 3 groups for statistical analysis (2010, 2011, 2012). We considered each year separately (2010, 2011, 2012) with all 3 trapping areas pooled because sample sizes were too small to consider each trapping area separately. We conducted subsequent analyses on subsets of 2010 to investigate the role of biases in sample size and age. To test the influence of sample size, we randomly selected individuals from 2010 ($n = 169$) via the R (R Core Team 2013) command sample to create 100 subsets for each year that had the same sample sizes as 2011 and 2012 ($n = 77$ or 65). For age bias, we also ran all analyses with only yearlings and adults (71, 37, and 55 in 2010, 2011, and 2012, respectively) to investigate if the inclusion of pups skewed results.

Laboratory Methods

Wildlife Genetics International (Nelson, British Columbia, Canada) conducted much of the laboratory procedures including extraction and microsatellite amplification. Animals from 2010–2012 initially shared genotypes from 5 microsatellite loci (REN233H01, REN94H15, REN144A06, REN210D03, REN262I12; Breen et al. 2001) evaluated by Wildlife Genetics International, so we added an additional 3 loci to the datasets from all 3 years (2010–2012; REN68B08, REN85N14, Breen et al. 2001; AHT121, Holmes et al. 1995) to increase power for subsequent analyses. Technicians conducted polymerase chain reactions (PCR) for the 3 additional primers in 12-uL volumes with 20 ng of genomic DNA, 10× Amplitaq PCR buffer, 10× bovine serum albumin, 1.5 nM of $MgCl_2$,

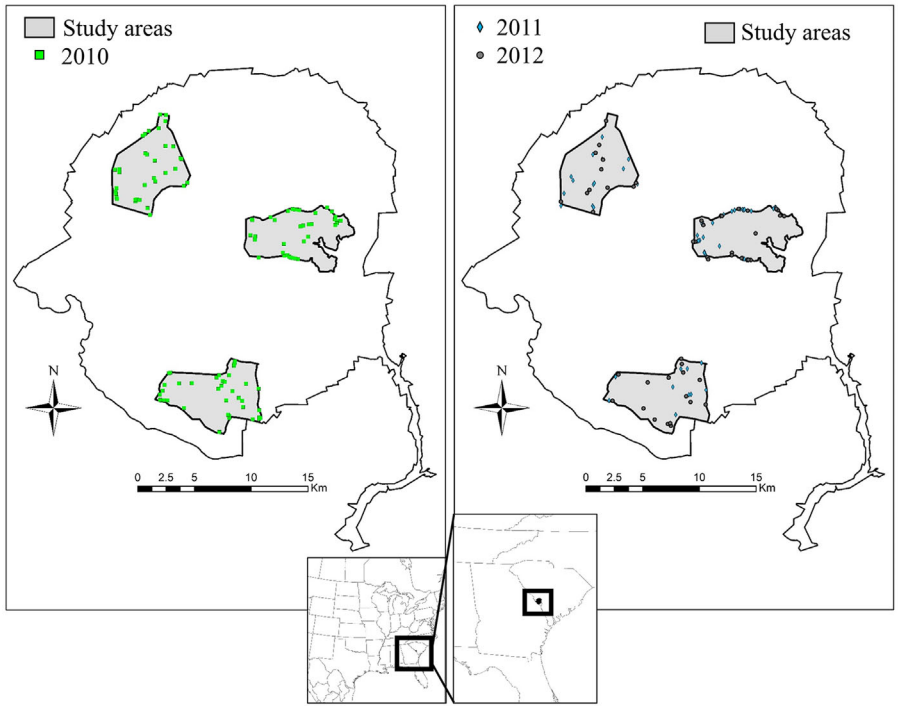

Figure 1. Spatial distribution of trapped coyotes across the 3 study areas on the Savannah River Site (SRS), South Carolina, USA. Coyotes were trapped for 3 years (2010, 2011, and 2012) across 3 study areas (light gray).

0.2 nM of each dNTP, 5 pmol of each primer, and 0.5 U of Amplitaq Gold (Life Technologies, Grand Island, NY, USA). Amplification conditions consisted of an initial 5 minute denaturation at 95°C followed by 20 cycles of touchdown PCR cycles at 95°C for 30 seconds, 65°C for 30 seconds with a −0.5°C drop each cycle, and extension at 72°C for 30 seconds, then 20 cycles of standard denaturation (30 sec at 95°C), annealing (30 sec at 55°C), and extension (30 sec at 72°C), and concluded with a final extension at 72°C for 5 minutes. Technicians amplified products on an ABI 3170 Genetic Analyzer, and alleles were scored in GeneMapper (Life Technologies).

For quality control, we randomly selected 30% of all homozygotes and 10% of heterozygotes within each year and re-genotyped those individuals across the 3 loci. The re-runs did not result in any mismatching genotypes. Additionally, we used the program MICRO-CHECKER (van Oosterhout et al. 2004) to estimate if null alleles were present at each locus.

Population Differentiation and Genetic Diversity

The signature of genetic differentiation of coyotes within our study areas in the years subsequent (i.e., 2011 and 2012) to the initial coyote removal (i.e., 2010) can provide critical insights into the spatial extent of coyote population structure on the SRS. To identify population differentiation between pre- and post-trapping periods, we used the Bayesian clustering program, STRUCTURE 2.3.4 (Pritchard et al. 2000) to delineate coyotes into genetic clusters (K) using the entire pooled dataset across study areas and years. Each STRUCTURE run (10 runs per K for $K = 1$–10) consisted of 100,000 burn-in followed by 100,000 permutations. We used highest likelihood from $K = 1$ to $K = 10$ and the ΔK method (Evanno et al. 2005) to determine the most likely K.

To complement the STRUCTURE analysis, we also calculated F_{ST}, a measure of genetic differentiation, between years (2010, 2011, and 2012) in the R package diveRsity (Keenan et al. 2013). Another potential source of genetic differentiation between coyotes is isolation-by-distance (IBD), a phenomenon where genetic differentiation increases with geographic distance (Wright 1943). We tested for IBD within all 3 years and subsets via Mantel tests between matrices of proportion of shared alleles (D_{PS}; Bowcock et al. 1994) and Euclidean distances between all individuals. We conducted Mantel tests in the R package vegan via the function mantel (Oksanen et al. 2017).

We used the R package diveRsity to calculate deviations from Hardy–Weinberg Equilibrium (HWE) and linkage equilibrium (LE) and metrics of genetic diversity in all years separately. Genetic diversity metrics included F_{IS} (inbreeding coefficient), observed and expected heterozygosities (H_O and H_E), and allelic richness (A_R). The function divBasic in diveRsity provides 95% confidence intervals around each diversity metric, allowing direct comparisons between years. We calculated all 95% confidence intervals via 10,000 permutations in diveRsity. The nature of effects of trapping on overall measures of genetic diversity in the post-removal years would depend on the spatial extent of genetic subdivision of the coyote population across the SRS. For example, we would expect an increase in genetic diversity compared to 2010 within the recolonized, post-removal population if immigrants were from genetically

differentiated coyote sources versus simply other areas within a single population.

Familial Structure

In addition to disruption of genetic structure, trapping may also alter the distribution of related individuals. Prior to trapping, we expected related coyotes to exhibit genetic signatures of philopatry (i.e., related individuals are found close together) as observed in other canids (Kitchen et al. 2005, DeYoung et al. 2009, Stronen et al. 2012). Thus, we expected trapping of resident animals to alter the genetic signature of philopatry between pre- and post-trapping years, especially if the recolonizing coyotes were unrelated transients.

Genetic spatial autocorrelations statistically evaluate if individuals within *a priori* defined distance intervals are more or less genetically similar than random, and thus, have been a popular test to investigate fine-scale genetic structure created by philopatry (Banks and Peakall 2012). Spatial autocorrelation coefficients (r; Peakall et al. 2003) between proximate individuals should be significantly positive if philopatry is strong within each year. Peakall and Banks (2012) recommend testing multiple distance intervals, so we evaluated 500-m to 5-km intervals for each year and sexes within each year separately in GenAlEx version 6.2 (Peakall and Smouse 2006). Regardless of the distance interval used, patterns were consistent across years and sexes. Although we tested 500-m to 5-km intervals as potential distance intervals, 1 km was the finest distance interval that had sufficient sample sizes to conduct the analysis at close distances (<5 km). Therefore, we used 1-km distance intervals for all spatial autocorrelation and subsequent analyses with dispersal distances.

Although we expected the genetic signature of residual familial structure subsequent to culling to be diluted by an influx of transient individuals into the trapped area, changes in the attributes of natal dispersal (e.g., distances, rates) of coyotes within and around the culled area also may dictate how familial structure is preserved or degraded within the zone of population reduction. For example, dispersal away from natal ranges increased following culls in European badgers (*Meles meles*), which in turn decreased the strength of local spatial autocorrelation (Pope et al. 2007). To investigate how dispersal distances may have been influenced by the culling of coyotes in the post-removal periods (i.e., 2011 and 2012), we used the program BadMove 1.0 as implemented in Pope et al. (2007).

BadMove estimates the displacement distance (D), the distance between where the animal was sampled (i.e., observed spatial coordinates) and a predicted location based on its genotype and underlying spatial variation in the population (Wasser et al. 2004). Calculation of D for each individual involves estimation of 2 parameters within a Gaussian weighted function based on a training dataset. The first parameter is related to the strength of IBD (s), and the second is a constant (c) that ensures that all individuals more than c standard deviations away from the focal point influence the expected allele frequencies equally (Wasser et al. 2004, Pope et al. 2007). Essentially, D is an estimated dispersal distance based on the observed allele frequencies. Pope et al. (2007) reported that D accurately predicted dispersal distances in European badgers, but dispersal distances for coyotes may exceed our study area (max. distance between coyotes = 30.2 km, dispersal distances can exceed 100 km; Harrison 1992). Therefore, we focused on the proportion of inferred Ds instead of actual length to examine if the frequency of philopatric individuals decreased following trapping.

To calculate D, we chose the extension BadMovePerm for our analyses because of the differences in sample sizes between our pre- and post-trapping datasets. BadMovePerm controls for sample size differences by subsampling each dataset and repeating the procedure to produce confidence intervals around each D. We used BadMovePerm to compare differences in distances between the initial culling period and each of the 2 post-trapping datasets (2011 and 2012). Each run in BadMovePerm included a training dataset (2010) and a single post-trapping dataset (2011 or 2012), resulting in 2 separate runs. Each run included 100 permutations to estimate confidence intervals around each D value. Therefore, we estimated D twice for 2010 and once per post-trapping period (2011 and 2012). We conducted all analyses on the full datasets and yearling and adult animals only because the inclusion of pups that had not dispersed may have biased our estimates.

For statistical analysis, we focused on the proportion of individuals with a $D < 5$ km within each of the 100 permutations (distance intervals tested: <1, <2, <3, <4, and <5 km). We then used these 100 data points for D and proportion of $D < 5$ km from each of the 3 sampling periods (2010, 2011, 2012) to evaluate whether changes in the attributes of dispersal had occurred in the post-trapping sampling periods. We limited statistical tests to within a single BadMovePerm run because of the correction for sample sizes. Therefore, we conducted all pair-wise tests (pre- vs. post-trapping) for average D using 2-sample t-tests within R, resulting in 18 t-tests for the proportion of individuals with $D < 5$ km. We used 5 distance intervals (<1, <2, <3, <4, and <5 km) within each of the 3 BadMovePerm runs to mimic the distance intervals of the spatial autocorrelations. We acknowledge that these distance intervals are somewhat arbitrary given the small spatial scale of this study, but we did not observe an overrepresentation of small D values from 0–30 km in any runs. Therefore, it does not appear that our sampling biased inferred D values toward small values. We expected that if dispersal distances increased following the initial culling, the proportions of individuals with $D < 5$ km should be lower in post-trapping datasets (2011, 2012) than was observed in the pre-trapping period (2010).

Simulations of Compensatory Immigration

Our simulations were specifically designed to evaluate if and when our statistics could detect changes in genetic structure created by compensatory reproduction and immigration. Therefore, we created simulated populations to mimic

varying levels of compensatory immigration following trapping of 75% of the coyotes each year (as estimated in Kilgo et al. 2014). We generated simulated populations in the program CDPOP version 2.3 (Landguth and Cushman 2010), a spatially explicit gene flow simulation program that allows control over dispersal regimes, mortality, and other demographic processes. The first step involved simulating populations before trapping (i.e., 2010), so we ran CDPOP for 40 generations (coyotes were first recorded on SRS in the 1986; Schrecengost et al. 2009). Program CDPOP requires extensive parameterization for biological factors, so we attempted to mimic population processes in expanded coyote populations, particularly those with limited trapping as observed on SRS prior to 2011.

All simulated populations had 311 individuals so that all individuals had identical spatial coordinates to the observed dataset. We also simulated smaller populations (100, 150, 200, and 250), but found no differences in the results (data not presented); therefore, we kept the original 311 individuals as the total population. Dispersal and mating movements occurred according to Euclidean distances between individuals, and dispersal occurred according to an inverse square distribution. Maximum dispersal distances were the largest distance between individuals (30.3 km) for both sexes. Sex ratios were equal, and mating was sexual with no replacement for either sex (coyotes pair bond during the mating season). We designated 3 age groups for breeding and mortality parameterization (Kilgo et al. 2017): juveniles (<0.5 yr old), yearlings (1.5 yr old), and adults (>2.5 yr old). Based on the first trapping set, >90% of breeding females were adults and had an average of 5 pups (Kilgo et al. 2017), so we limited breeding to adult females in our simulations. Mixed evidence has been found for differential juvenile mortality rates in southern coyotes (Windberg et al. 1985, Holzman et al. 1992), but given the small amount of trapping on SRS (i.e., one of the main reasons for higher mortality in juveniles; Windberg et al. 1985), we used the same mortality rate for all age classes (34.2%; Schrecengost et al. 2009). We assumed carrying capacity was the number of individuals (311 individuals) and population growth followed a logistic growth curve. We genotyped all populations at 8 microsatellite loci with 11 alleles ($\bar{x}$ alleles found in the 2010 dataset = 11.2). We saved genotype results at generation 40, and called resultant datasets collectively Simulated 2010 (2010_{sim}).

Program CDPOP allows for changes in demographic processes at designated generations, and in this case, we instituted higher mortality rates and age-specific reproductive rates based on field data collected in 2011–2012. To simulate trapping, mortality rates for all animals increased to 75% after generation 40. Unlike pre-trapping years, litter sizes increased slightly and all age classes bred (Kilgo et al. 2017). Therefore, juvenile coyotes had an average of 4 pups, yearlings had 5, and adults had 7 with standard deviations of 1 pup. We ran trapping simulations for 2 generations (i.e., 2 yr) and saved all simulated post-trapping populations (i.e., generations 41 and 42). Based on these simulations, we had 3 sets of 100 simulated populations: 100 simulated 2010 populations (i.e., 2010_{sim}) and 200 simulated post-trapping populations (i.e., 2011_{sim} and 2012_{sim}).

To simulate compensatory immigration, we added varying numbers of simulated un-related individuals to the sampled post-trapping populations. This process mimics adjacent individuals not subject to trapping immigrating into trapped areas. Because each simulated trapped population was generated based on allele frequencies of a unique pre-trapping population, we created 1,000 unrelated individuals for each population ($n = 200$) based on the allele frequencies from the last un-trapped generation (generation 40) in the program Kingroup version 2 (Konovalov et al. 2004). We simulated 11 levels of compensatory immigration (0, 10, 20, 30, 40, 50, 60, 70, 80, 90, and 100%) by replacing individuals within the sampled post-trapping populations with varying numbers of simulated unrelated individuals. With this method, we generated 2,200 simulated post-trapping populations (1,100 populations for both 2011 and 2012) in addition to the 100 2010_{sim} populations.

Statistical Analysis of Simulated Compensatory Reproduction and Immigration

The goal of these simulations was to create a gradient of compensatory immigration to identify when or if population genetics can identify an alteration in genetic structure following trapping. Thus, we ran all of our analyses (genetic differentiation, genetic diversity, and familial structure) on all of the simulated pre- and post-trapping datasets. We sampled each population ($n = 311$) by collecting individuals with the identical spatial coordinates as the observed dataset for each year, so sample sizes were the same in the simulated and observed datasets ($n = 169$ for 2010_{sim}, $n = 77$ for 2011_{sim}, $n = 65$ for 2012_{sim}). Although we tried to mimic the conditions of our simulations to the observed dataset, they were not directly comparable because the demographic processes underlying the simulations may not have exactly mimicked the SRS coyote population. Therefore, we could not directly estimate the amount of compensatory immigration occurring in the observed dataset based on the simulations, but we could deduce if our statistics could detect compensatory immigration.

Overall, the statistical analyses and expectations for each test were the same for the simulated populations as in the observed. We attempted to identify genetic differentiation between 2010_{sim} and simulated post-trapping years (2011_{sim}, 2012_{sim}), which would indicate an alternative genetic stock was present in the trapped areas due to compensatory immigration. For the other tests (genetic diversity and familial structure), we used linear mixed models to examine when compensatory immigration caused a significant change from 2010_{sim} populations. The percent compensatory immigration was the fixed effect, whereas we coded population (1–100) as a random effect. We ran each year separately (2011 or 2012 only) and tested whether compensatory immigration caused significant increases in genetic diversity (i.e., allelic richness and observed heterozygosities) and reduced spatial autocorrelation coefficients in

2011_{sim} and 2012_{sim}. Unlike genetic diversity and spatial autocorrelations, we did not expect changes in the proportion of individuals at local scales (<5 km) from BadMove because we did not alter maximum dispersal distances in the simulations.

We constructed linear mixed models in the R package lmerTest (Kuznetsova et al. 2016), which calculates *t* values, Satterthwaite approximation for degrees of freedom, and *P*-values for each fixed effect (i.e., multiple comparisons between 11 levels of compensatory immigration). We also calculated 2 measures of effect size ($\bar{x}$ differences and Cohen's D; Cohen 1962) for each pair-wise comparison between the simulated 2010 populations and each level of immigration ($n = 22$ tests, 11 for each simulated yr). We used 2 measures of effect size based on little *consensus* of appropriate effect size measures. Mean differences (i.e., raw difference between $\bar{x}$ of 2010_{sim} and 2011_{sim} or 2012_{sim}) provided an uncorrected measure in the units of each metric (Baguley 2009). Baguley (2009) argues that uncorrected effect sizes are independent of variance, in the units used within the study, and easier to compute, making them superior in most cases to standardized metrics. In contrast, Cohen's D is the most widely used effect size measure (Fritz and Morris 2012), so interpretation is more straightforward in comparison with other studies. Cohen's D specifically standardizes across the pooled standard deviation between 2 groups (Cohen 1962, 1994).

RESULTS

Population Differentiation and Genetic Diversity

Overall, STRUCTURE indicated the most likely *K* was 1 (likelihood = −9,611.2), indicating that there was no evidence of structure among study areas or over years within or among study areas. The highest ΔK occurred at $K = 2$ ($\Delta K = 1.272$), but assignments to each cluster were weak (*q*-values = 0.35–0.75). The F_{ST} values between years (using data pooled across study areas within years) were low (0.000–0.001) and not significant ($P = 0.119$–0.494) regardless of the pair-wise comparison. Measures of population differentiation were also low for all the subset groups ($F_{ST} = 0.000$–0.005, all $P > 0.165$). We detected weak IBD in 2010 (Mantel $r = 0.036$, $P = 0.002$), but not in 2011 and 2012 (all Mantel $r < 0.026$, all $P > 0.125$).

Genetic diversity measures were similar across all 3 years with no significant differences between years according to calculated 95% confidence intervals (Table 1). Allelic richness, for example, ranged from 9.34 to 10.11 alleles/locus. No locus consistently deviated from either HWE or LE in any grouping, and 95% confidence intervals for F_{IS}

Table 1. Genetic diversity metrics of 8 microsatellite loci for coyotes trapped from 2010–2012 at the Savannah River Site, South Carolina, USA. Diversity metrics include observed (H_O) and expected (H_E) heterozygosities and allelic richness (A_R), a measure of the number alleles corrected for sample size. Our final diversity metric is F_{IS} (inbreeding coefficient) where positive F_{IS} values indicate an excess of homozygotes within each group (i.e., lower H_O than H_E). No diversity metrics differed across all loci or years according to the 95% confidence intervals (provided for F_{IS} values) calculated in diveRsity.

Microsatellite locus	*n*	H_O	H_E	A_R	F_{IS}	F_{IS} low	F_{IS} high
2010							
REN68B08	169	0.86	0.86	12.18	−0.003	−0.067	0.061
REN85N14	164	0.83	0.85	12.04	0.027	−0.037	0.088
AHT121	168	0.75	0.85	14.40	0.123	0.004	0.196
REN233H01	169	0.83	0.79	7.51	−0.043	−0.114	0.022
REN94H15	169	0.85	0.84	10.63	−0.012	−0.066	0.044
REN144A06	169	0.79	0.77	9.72	−0.027	−0.104	0.050
REN210D03	169	0.77	0.77	5.96	0.005	−0.076	0.087
REN262I12	169	0.67	0.73	8.42	0.072	−0.019	0.158
Overall	169	0.79	0.81	10.11	0.018	−0.009	0.039
2011							
REN68B08	77	0.77	0.86	9.00	0.105	−0.009	0.216
REN85N14	76	0.79	0.84	10.80	0.062	−0.039	0.168
AHT121	77	0.81	0.83	11.88	0.028	−0.069	0.124
REN233H01	77	0.79	0.81	7.73	0.017	−0.099	0.120
REN94H15	77	0.87	0.83	11.23	−0.043	−0.136	0.046
REN144A06	77	0.70	0.74	9.74	0.055	−0.061	0.160
REN210D03	77	0.74	0.77	5.97	0.044	−0.077	0.164
REN262I12	77	0.64	0.74	8.36	0.143	−0.003	0.278
Overall	77	0.76	0.80	9.34	0.050	−0.001	0.083
2012							
REN68B08	65	0.86	0.83	8.97	−0.043	−0.140	0.046
REN85N14	65	0.89	0.86	11.54	−0.042	−0.135	0.040
AHT121	65	0.74	0.88	13.82	0.112	−0.048	0.165
REN233H01	65	0.85	0.79	7.51	−0.066	−0.166	0.039
REN94H15	65	0.74	0.81	9.78	0.091	−0.045	0.221
REN144A06	65	0.77	0.81	9.48	0.047	−0.077	0.171
REN210D03	65	0.75	0.79	7.29	0.045	−0.086	0.170
REN262I12	65	0.78	0.77	9.12	−0.026	−0.154	0.098
Overall	65	0.80	0.82	9.69	0.022	−0.022	0.051

values included zero in all but one case (AHT121 in 2010). MICRO-CHECKER found no evidence for null alleles in any grouping.

Familial Structure

In 2010, we found positive spatial autocorrelations for individuals within 2 distance intervals: 0–1 km ($r = 0.066$, $P = 0.001$) and 1–2 km ($r = 0.015$, $P = 0.003$; Fig. 2a). All other distance intervals <5 km did not deviate from random. The strongest spatial autocorrelation in the 2010 sampling period occurred for individuals separated by 0–1 km. The post-trapping years, 2011 and 2012, exhibited significant positive spatial autocorrelations at the 0–1 km distance interval (2011: $r = 0.031$, $P = 0.003$; 2012: $r = 0.040$, $P = 0.011$; Fig. 2) but not at 1–2 km. These results were confirmed by the subsets for ages and sample sizes because the significant relationships detected for the entire 2010 dataset remained for spatial autocorrelations in all 200 subset groups. Only 2010 remained significant at the 0–1-km interval (2010: $r = 0.085$, $P = 0.001$, 2011: $r = 0.039$, $P = 0.156$, 2012: $r = 0.041$, $P = 0.061$) when we analyzed only yearlings and adults.

We observed highly similar D values for 2010 across both runs and for each subset group in BadMovePerm, which suggests high consistency across runs regardless of the included post-trapping dataset. Proportions of coyotes with a $D < 5$ km in 2010 were similar to those of coyotes in 2012 at all distance intervals examined (all $t < 1.86$, all $P > 0.064$). In contrast, 2011 had a lower proportion of coyotes than 2010 at all distance intervals: <1 km ($t = 2.44$, $P = 0.016$), <2 km ($t = 2.15$, $P = 0.032$), <4 km ($t = 2.85$, $P = 0.005$), and <5 km (all $t > 2.15$, all $P < 0.032$; Fig. 3). For adults only, 2010 had a greater proportion of coyotes with $D < 1$–5 km than both 2011 (all $t > 2.08$, $P < 0.039$) and 2012 (all $t > 3.36$, all $P < 0.009$) regardless of the distance interval (Fig. 3). Although we did not statistically examine the average D because of the fine scale of our study, trapped coyotes had an average D from 17.31 km to 20.45 km across 3 years. These values were under the maximum distance across our study area, but this is likely a function of the sample area size.

Statistical Analysis of Simulated Compensatory Reproduction and Immigration

Compensatory immigration affected our statistics in different ways, but we observed little change in STRUCTURE and allelic richness. STRUCTURE always found a single population regardless of the level of compensatory immigration (all $\Delta K < 5.021$). Allelic richness also did not change between simulated pre-trapping (i.e., generation 40) and either post-trapping year (all $t = -0.94$–0.47, all $P > 0.200$), and had the smallest effect sizes in all comparisons (all differences between means: −0.0188–0.0813, Cohen's D: −0.0942–0.3692; Table S1a, available online in Supporting Information).

Unlike STRUCTURE and allelic richness, compensatory immigration caused significant changes between simulated pre- and post-trapping years in observed

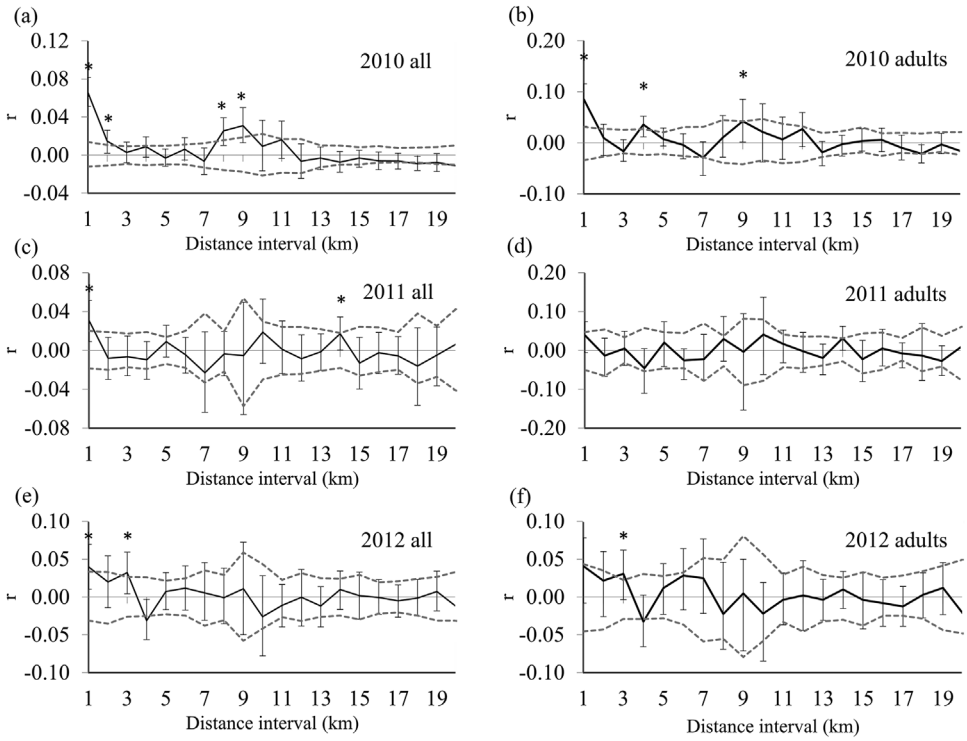

Figure 2. Spatial autocorrelations for all coyotes trapped in 2010 (a), 2011 (c), and 2012 (e) and adults only (2010: [b], 2011: [d], and 2012: [f]) on the Savannah River Site, South Carolina, USA. All groups had a significant, positive spatial autocorrelation coefficient (r) at 0–1 km, but 2010 had a higher r than the other groups. Significant positive spatial autocorrelations are denoted by an asterisk (*). Dotted lines correspond to 95% confidence intervals calculated via 1,000 permutations and error bars are based on 1,000 bootstraps.

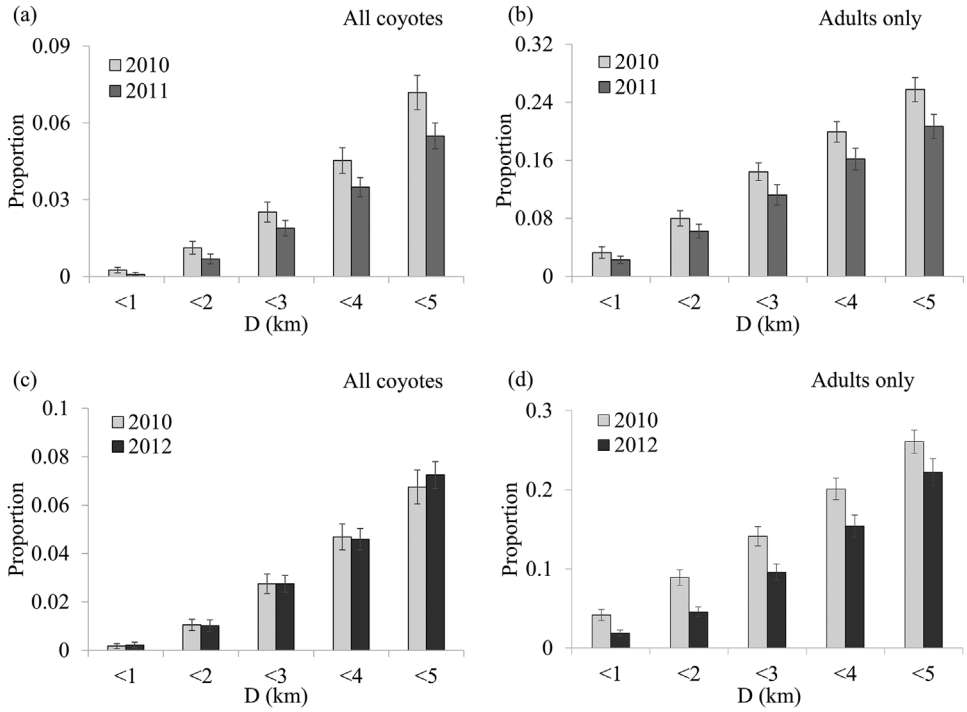

Figure 3. The proportion of all coyotes and adults only trapped on the Savannah River Site, South Carolina, USA, with a displacement distance (D) < 5 km across 2 runs in BadMovePerm. Each run had a training dataset (2010; light gray) compared with a post-trapping dataset (2011 or 2012; dark gray). In 2011, proportions of coyotes trapped <5 km from their predicted natal range were significantly smaller than 2010 in all coyotes (a) and only adults (b) but not in 2012 (all [c] adults [d]). All error bars represent 95% confidence intervals calculated via 100 permutations.

heterozygosity, spatial autocorrelation coefficients, and BadMove results. As expected, compensatory immigration increased observed heterozygosity (Fig. 4), but values were significantly different only from the simulated 2010 populations and 0% immigration when immigrants comprised >60% of the population (2011_{sim}: all $t > 3.25$, all $P < 0.001$, 2012_{sim}: all $t > 3.96$, all $P < 0.001$). Similarly, effect sizes for the 0–50% immigration were smaller ($\bar{x}$ differences: −0.0088–0.0078, Cohen's D: −0.7624–0.6960) than those with 60–100% immigration ($\bar{x}$ differences: −0.0244 to −0.0130, Cohen's D: −2.4572 to −1.2488; Table S1b).

Spatial autocorrelation coefficients at the 0–1-km distance interval were the most sensitive to the addition of unrelated immigrants. Even at 10% immigrants, spatial autocorrelation coefficients were significantly less than the un-trapped populations in 2011_{sim} and 2012_{sim} (10% immigration vs. 2010_{sim} and 0% immigrants with trapping mortality: $t = -4.72$ to -5.10, $P < 0.001$; Fig. 4). Effect sizes were also the largest for spatial autocorrelations ($\bar{x}$ differences = 0.0189–0.0299, Cohen's D = 1.0991–7.5931; Table S1c). Like spatial autocorrelation coefficients, compensatory immigration decreased the proportion of $D < 5$ km in both post-trapping years ($t = -4.25$ to -11.15, $P < 0.001$), even at 10% compensatory immigration (Fig. 5). Surprisingly, even 0% immigration was different from un-trapped populations for 2011, but the effect sizes generally increased as immigration increased (0% immigration: $\bar{x}$ differences = 0.0450–0.0705, Cohen's D = 0.3135–0.7720 vs. 100% immigration: $\bar{x}$ differences = 0.1812–0.1950, Cohen's D = 2.1553–2.1886; Table S1d).

DISCUSSION

Based on the empirical and simulated datasets, coyotes can recover from lethal trapping via immigration and reproduction. Increasing immigration had the largest impact on genetic measures of genetic diversity and familial structure, whereas population differentiation remained unchanged in our simulations. Changes in familial structure, in particular, were sensitive to increasing immigration, making it a powerful tool for understanding how mesocarnivores may recover from lethal control. Our simulations also found that despite our relatively low number of markers and unequal sample sizes between pre- and post-trapping periods, our methods could detect changes in genetic structure due to compensatory immigration.

Roles of Compensatory Immigration and Reproduction

Our analyses suggest that immigration contributed substantially to population recovery of coyotes in our study area subsequent to the intensive removal program conducted in 2010. We found weakened signals of philopatry in post-trapping years, which are indicative of recolonization by transient animals into the newly vacant territories. Our simulations of compensatory immigration indicated that spatial autocorrelations were most sensitive to compensatory immigration (i.e., 10% immigration caused a significant decrease in r), and both 2011 and 2012 had lower spatial

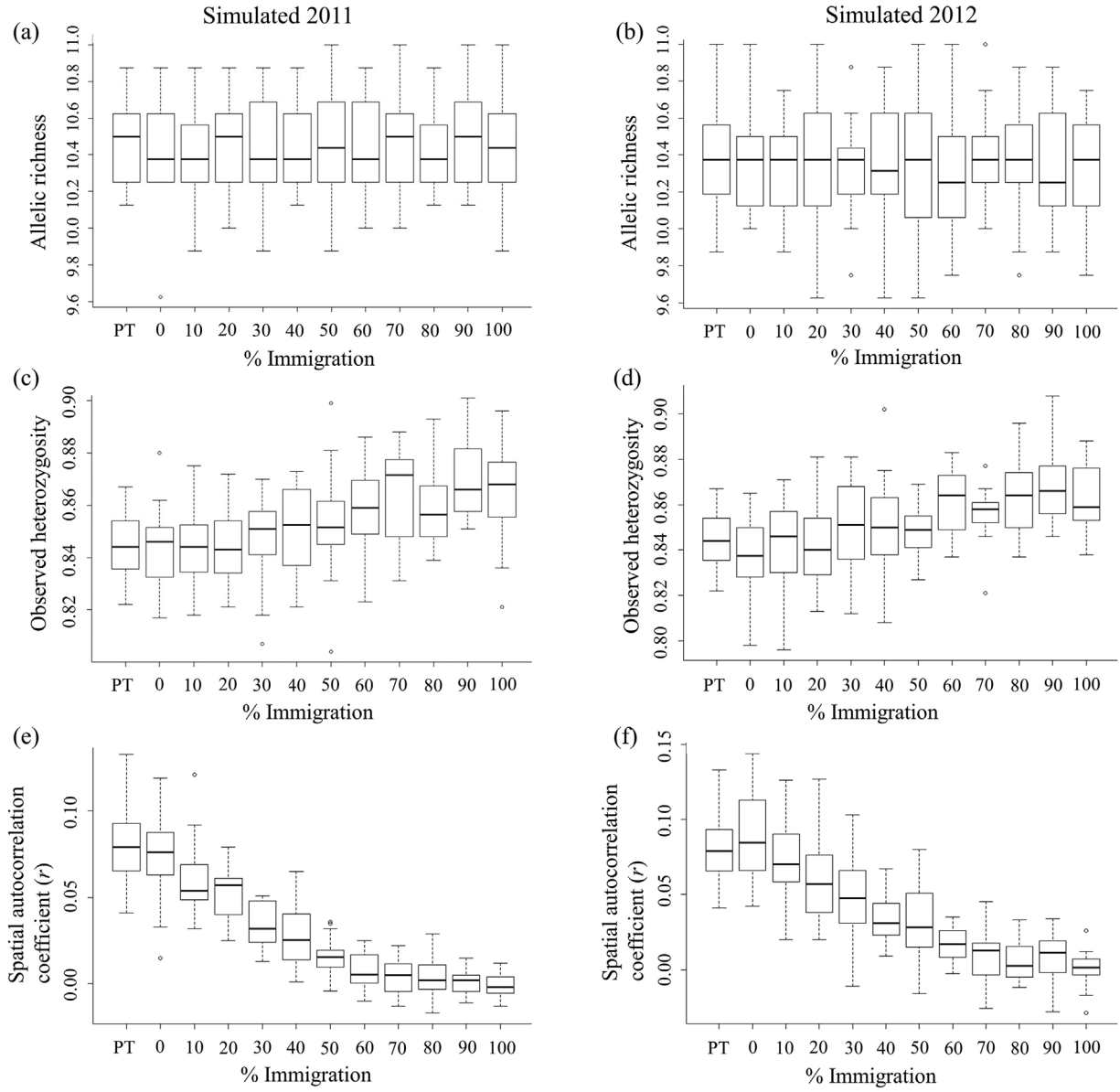

Figure 4. Results of simulations of increasing compensatory immigration (PT = pre-trapping, 0–100% immigrants in sample) for tests of genetic diversity and spatial autocorrelations in simulated trapping of coyotes on the Savannah River Site, South Carolina, USA, 2011 and 2012 (Simulated 2011 and 2012). All statistical analysis compared simulated 2010 (pre-trapping; PT) with increasing levels of compensatory immigration (0–100%). Allelic richness (a, b) did not change across varying levels of immigration, but observed heterozygosity (c, d) had a positive relationship with level of immigration. Spatial autocorrelation coefficients (e, f) were the most sensitive to compensatory immigration, and steadily decreased with increasing levels of immigration. Linear mixed models found that H_O at 60% or greater immigration was significantly higher than PT and 0% immigration (all $t > 3.25$, all $P < 0.001$). Spatial autocorrelation coefficients at 10–90% immigration were significantly lower than PT and 0%. Median values for each group are in the middle of each boxplot (thick line) where the whiskers denote the top and bottom 25% of the 100 simulated populations (boxes contain 50% of the data). Outliers (i.e., those outside the whiskers) are open circles.

autocorrelation coefficients, especially after removing pups from the analyses. Our simulations indicated that for coyotes, BadMove cannot differentiate between compensatory immigration and increased dispersal. None of the changes in genetic structure from pre- and post-trapping periods were explained by sample size or age bias based on our sensitivity analyses or simulations; thus, coyotes appear to at least partially recover from intensive trapping via compensatory immigration.

Our data did not exhibit significant shifts in genetic diversity between pre- and post-trapping years, which implies that all immigrants to trapped areas came from a single genetic source. A change in the genetic attributes of the recolonized population would occur only if immigrants were genetically differentiated from the pre-removal populations, regardless of the number of sources (Abdelkrim et al. 2007, Russell et al. 2009, Veale et al. 2013). Our genetic differentiation analyses did not support multiple genetic populations, so it is likely coyotes in the SRS region are a single, panmictic population. Our simulations demonstrated that in cases of high compensatory immigration (>60% of sampled individuals are

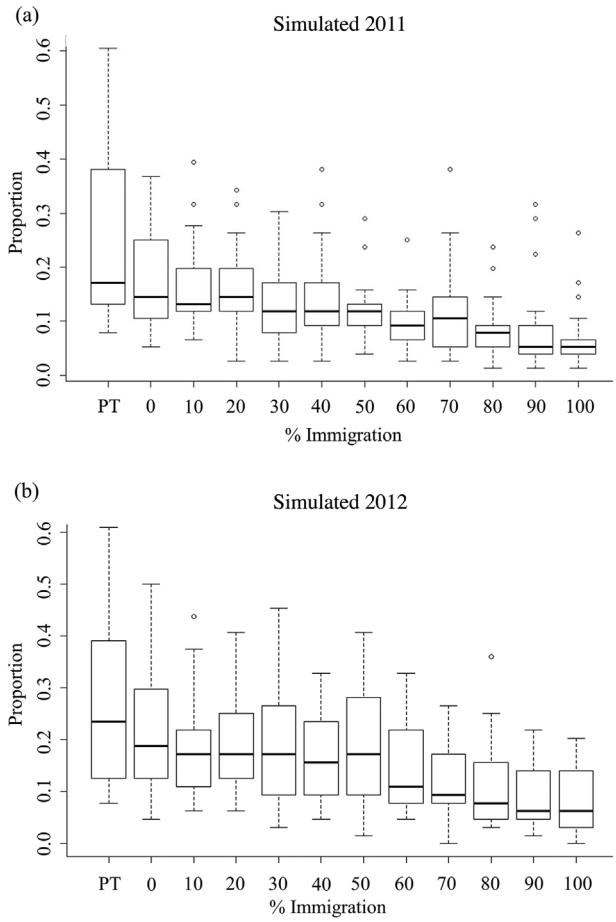

Figure 5. Proportion of displacement distances (D) < 5 km in simulated trapping of coyotes on the Savannah River Site, South Carolina, USA, 2011 (a) and 2012 (b). BadmovePerm calculated D based on simulated 2010 (pre-trapping; PT) and either simulated 2011 or 2012 with increasing levels of compensatory immigration (0–100%). Linear mixed models indicated that the proportion of $D < 5$ km decreased with increasing compensatory immigration from 10–100%. Boxplots contain the median values for each group (thick line), interquartile range (boxes, 50% of data), and whiskers (top and bottom 25% of the 100 simulated populations). Open circles denote outliers in each group.

migrants), observed heterozygosity will increase, whereas allelic richness will not.

Although we found evidence for compensatory immigration, our simulations suggest that compensatory immigration was not completely responsible for coyote recovery following trapping. Exploited coyote populations typically exhibit larger litter sizes than undisturbed populations (Knowlton 1972, Berg and Chesness 1978, Davison 1980, Andelt et al. 1987), which are the result of decreased competition for food or younger breeding ages (Andelt et al. 1987). We did not record large increases in litter size (Kilgo et al. 2017), but another compensation mechanism is for animals to breed at younger ages. Indeed, coyotes on SRS bred at younger ages where although rarely, even individuals <1 year old conceived litters. Prior to trapping, no juveniles were detected as breeding and the yearling pregnancy rate was low on SRS (Kilgo et al. 2017). Younger breeding ages are fairly typical in intensively trapped canids (Harris and Smith 1987, Knowlton et al. 1999, Gese 2005, Minnie et al. 2016), so coyotes likely compensated by breeding at younger ages.

A number of mechanisms could influence how compensatory immigration and reproduction occur following trapping, but Gese et al. (1989) suggested that coyote dynamics are regulated by social intolerances mediated by resource availability. Therefore, if a given habitat is saturated with territorial coyotes, transient coyotes likely would be forced into vacant habitats, such as those with high mortality (i.e., trapped areas), should they become available for occupation. Previous studies on SRS reported that coyotes reach relatively high densities compared to other populations, have larger home ranges than other southeastern populations, and do not appear to form well-defined packs (Schrecengost et al. 2009), so immigration of transient coyotes into trapped areas may be high because the landscape is already saturated. Transients have been reported to account for ≥30% of coyote populations (Windberg and Knowlton 1988, Chamberlain et al. 2000). Hinton et al. (2015) reported that 14 of 28 radio-collared coyotes in a North Carolina, USA population were transients and 7 of the transients established residency during the study when a territory holder was killed. Similarly, reproductive output of the remaining animals will increase, which is consistent with the somewhat greater litter sizes of adults and the greater frequency of juveniles breeding following trapping (Kilgo et al. 2017). Both increased immigration and younger ages of breeding are common responses to trapping in other trapped species (Beasley et al. 2013, Robinson et al. 2014, Lieury et al. 2015, Minnie et al. 2016). Like previously studied mesocarnivores, the greater number of animals breeding combined with high immigration rates ensure that coyotes will likely recover quickly, which could easily undermine control efforts within the southeastern United States.

Population Genetics and Simulations as a Monitoring Tool Following Trapping

Monitoring populations such as coyotes after trapping presents a number of challenges, including limited sample size and spatial scale, but remains critically important for designing effective control strategies (Lieury et al. 2015). Population genetics offers a powerful tool to detect changes in genetic structure following trapping, but investigators need realistic expectations of how demographic changes will affect genetic structure. In cases where a separate genetic stock replenishes culled populations (e.g., island rodent eradication; Veale et al. 2013), these expectations are fairly simple to define because a separate genetic population introduces new alleles and is genetically divergent from the original population. In many genetic analyses, detecting underlying patterns increases with the amount of genetic differentiation (Latch et al. 2006). Most control situations, however, involve continuous populations like coyotes where genetic differentiation is small and the study area does not function as an island. Therefore, simulations are critical to investigate how genetic structure may change under various demographic scenarios such as differing levels of compensatory immigration.

Simulations are rapidly becoming essential for analysis of population genetic data because they allow for control of underlying processes such as dispersal regimes, population sizes, and mating strategies (Hoban et al. 2012). In cases of wild populations, a number of biases including small sample sizes, age biases, and clustered sampling often exist in resultant datasets, but it is difficult to assess the potential impact of such biases via empirical datasets. Instead, simulations allow for explicit testing of these potential biases (Schwartz and McKelvey 2009, Oyler-McCance et al. 2013, Kierepka and Latch 2016), which can help authors separate statistical artifacts from biologically relevant processes (e.g., compensatory immigration). The growing number of spatially explicit programs such as CDPOP that allow parameterization to match observed populations has increased the accessibility of simulations outside of programmers, and we highly recommend their increased use in monitoring projects.

Despite the obvious benefits to simulations paired with population genetics within trapping studies, there are a number of caveats that should be addressed in future studies. One important consideration is to not assume simulated populations are directly comparable to an empirical population because demographic processes and their effect on genetic variation within an empirical population are difficult to replicate in simulations. For example, all microsatellite loci within the initial population are assumed to have the same starting number of alleles, which was the main reason that our simulated datasets were not directly comparable to our empirical datasets. Another potential drawback of simulations is that most simulation programs require extensive parameterization of life-history traits such as age structure, mortality rates, dispersal regimes, and carrying capacity. Many of these factors can be estimated via field data, but using expert opinion or best guesses may not accurately represent reality. Many trapped populations are generalist species with high degrees of plasticity in behavior, which may further complicate parameterizing simulations from other study areas. Based on these potential pitfalls, authors should interpret simulations carefully, but even with uncertainty, we recommend simulations be used for assessing statistic performance given potential sampling biases (Kierepka and Latch 2016) and investigating power of genetic analyses to detect changes in genetic structure according to management or demographic processes.

MANAGEMENT IMPLICATIONS

Despite intensive local trapping, coyotes appear to recover quickly via compensatory reproduction and immigration. Therefore, coyote control alone may not be a feasible solution for boosting deer recruitment in high coyote density areas like SRS. Given the large home ranges of mesopredators such as coyotes, extending the spatial scale of control efforts is often not feasible because of financial and ethical reasons. We recommend further evaluation of multiple control strategies (Blejwas et al. 2002, Lieury et al. 2015) and population dynamics pre- and post-trapping (e.g., timing of dispersal and speed of recovery). Population genetics can be a powerful technique to monitor population dynamics pre- and post-trapping, but we advocate the use of simulations and sensitivity analyses as performed in this study to evaluate power and potential biases due to sampling. Experimental studies and monitoring via field and genetic techniques could then help tailor control efforts to maximize their effectiveness in the face of compensatory mechanisms (Lieury et al. 2015).

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