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TEMPORAL GENETIC VARIATION IN A COYOTE (*CANIS LATRANS*) POPULATION EXPERIENCING HIGH TURNOVER

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Temporal genetic variation was examined in a coyote (*Canis latrans*) population that experienced intensive removal for several decades. The population experienced separate periods of nonselective and selective control, and comparisons were made between control methods. Analyses at 11 microsatellite loci revealed only subtle genetic differences between removal regimes when analyzed by year of birth or resident status. Numbers of alleles per locus (4–16) and expected heterozygosities (0.617–0.915) were high across groups and few 1st-order relatives were detected within groups. Coyote social structure and dispersal patterns appear to adequately maintain genetic variation and promote genetic homogeneity over relatively small geographic scales during periods of locally aggressive removal.

Key words: *Canis latrans*, coyote, genetic variation, microsatellite, population structure, temporal variation

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Coyotes (*Canis latrans*) are mobile, adaptable canids found in a wide range of habitats across North America, with range extensions into previously unoccupied areas in the western and eastern United States. Although long-distance dispersal capabilities in both sexes (Harrison 1992) and relatively large proportions of transient coyotes that do not exhibit fidelity to a single territory (typically 13–34% of a population—Andelt 1985; Windberg and Knowlton 1988) suggest that coyotes exist as a panmictic population, other aspects of coyote behavior may increase the likelihood of local population structure.

Coyotes seem to occur in clusters of contiguous territories, the spacing of which can be broken by unsuitable habitat such as dense forest or marshland. Coyote breeding pairs defend mutually exclusive territories in which they raise a single litter of pups every year. The ''alpha'' breeding pairs dominate annual reproduction and may remain in a territory over a number of years (Andelt 1985; Gese et al. 1996; Sacks et al. 1999a). The alpha breeding pair may tolerate the presence of additional, nonbreeding ''beta'' coyotes (presumably offspring from the previous 1–2 years) in the territory, leading to formation of resident packs (Andelt 1985; Gese et al. 1996; Sacks et al. 1999b). These resident coyote packs also may remain faithful to sites over time (Kitchen et al. 2000a). Beta pack members related to, and associated with, territorial coyotes may have a competitive advantage over transient coyotes in attaining breeding status. Attainment of breeding status by pack associates (Gese et al. 1996) suggests potential inbreeding within packs. This would differ from other group-living canids where mates were found to be unrelated

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(e.g., wolves [*Canis lupus*]—Smith et al. 1997 and kit foxes [*Vulpes macrotis*]—Ralls et al. 2001).

There have been few genetic studies on coyote populations. Lehman and Wayne (1991) reported no significant geographical genetic structure (genetic subdivision) in coyotes using mitochondrial restriction data. Roy et al. (1994) also reported no evidence of population subdivision but identified limited inbreeding within coyote populations using microsatellite loci. However, Hamilton and Kennedy (1986) and Peppers et al. (1996) did detect some population structure across portions of the species' range using allozymes, including on a fine geographical scale.

Temporal aspects of coyote genetic variation have not been reported previously. Breeding populations, in general, are often assumed to have temporally stable allele frequencies. However, high mortality, lowered recruitment, or changes in breeding behavior resulting in reduced effective population size could interfere with such temporal genetic stability. For example, informative local temporal genetic variation has been detected in mule deer (*Odocoileus hemionus*—Scribner et al. 1991) populations, as well as in congregating wintering populations of American wigeon (*Anas americana*—Rhodes et al. 1993). Kin effects influencing recruitment or population structure, or social learning influencing survival (Garza et al. 1997; Hoglund et al. 1999; MacColl et al. 2000; Packer and Pusey 1982; Sacks et al. 1999a), also could result in local temporal genetic changes, although high dispersal capacities in coyotes imply that regional impacts may be small.

Management efforts, including removal, reintroductions, and translocations, have the potential to influence wildlife genetic structure (Scribner and Stüwe 1994; Serfass et al. 1998). Coyotes are managed intensely in some areas, particularly where they predate livestock, and in some populations annual removal exceeds 50%. Removal efforts typically are disruptive and coyotes in exploited populations may alter their behavior in response to such disturbances (Kitchen et al. 2000b). Demographic consequences of human exploitation include younger age structures, reduced adult survival rates, larger litter sizes, and smaller pack sizes (Knowlton et al. 1999), all of which can potentially influence local genetic structure. The type of control also may influence local gene dynamics. Most control efforts are nonselective, with all coyotes in an area targeted for removal, although certain nonselective removal methods may be biased toward certain age or sex classes. For example, oral sodium cyanide ejectors (M-44s) tend to remove more juveniles than they do adults (Sacks et al. 1999a), and calling-and-shooting appears to be biased toward males (Sacks et al. 1999a; Wagner 1997). Nonselective removal therefore may alter age and (at least temporarily) sex ratios, which in turn may influence subsequent recruitment or population dynamics (or both). In contrast, selective removal specifically targets breeding coyotes because evidence indicates that those animals are responsible for most livestock predation (Blejwas et al. 2002; Sacks et al. 1999a, 1999b). Elevated turnover of the breeding population resulting from selective removal theoretically could reduce genetic subdivision among populations by increasing the number of breeding vacancies filled by immigrants from the regional population. On the other hand, nonrandom filling of those breeding vacancies by increased recruitment of local animals (instead of transients or immigrants) may result in geographical and temporal genetic structuring. Both types of removal effort may lower coyote numbers, but what impacts they have, and whether genetic impacts differ by removal strategy, is unknown.

We examined genetic variation in coyotes over time, in a well-characterized population in northern California (Blejwas et al. 2002; Connor et al. 1998; Neale et al. 1998; Sacks et al. 1999a, 1999b). We were specifically interested in determining whether local

changes in genetic variation can be detected between periods of localized nonselective and selective removal efforts, as well as between resident and transient coyotes.

Materials and Methods

Study site, samples, and microsatellite genotyping.—Tissue samples were obtained between 1992 and 2000 from 104 coyotes at the Hopland Research and Extension Center (HREC) and portions of neighboring properties considered part of the research site. Tissues were frozen at −20°C until analysis. HREC is a 21.7-km^2 sheep research facility of the University of California in the Coast Range in Mendocino County, northern California. Since 1951, HREC has maintained a grazing flock of 900–1,500 ewes year round. In response to chronic coyote predation on lambs and ewes, 15–25 coyotes were removed nonselectively annually (from at least the early 1980s) from HREC and adjacent properties (Connor et al. 1998; Neale et al. 1998). Most samples were from United States Department of Agriculture Wildlife Services removal efforts, and the rest were obtained in the course of other studies on the site (Blejwas et al. 2002; Sacks et al. 1999a, 1999b). Coyote control was suspended during April 1993–March 1994 to allow live-capture of coyotes for a radiotelemetry study (Sacks et al. 1999a). Beginning in November 1995, HREC switched to a selective control strategy, and during the next 3 years only individuals or pairs known to be predating livestock were removed (Blejwas et al. 2002). After the radio telemetry study ended in August 1998, a mix of selective and nonselective control methods was employed. Radiocollared animals were studied extensively (Blejwas et al. 2002; Sacks et al. 1999a, 1999b) but were not excluded from removal efforts.

Deoxyribonucleic acid (DNA) isolations were performed using Qiagen's tissue kit and the manufacturer's protocol (Qiagen Inc., Valencia, California). Fifty nanograms of DNA was amplified in 1× amplification buffer, 0.5 units Amplitaq Gold (Applied Biosystems, Foster City, California), 1.5 mM $MgCl_2$, and 3 μM locus-specific primers, with 1 primer of each pair fluorescently labeled. Annealing temperatures of 45–55°C were used for all loci (CX2235, FH2010, FH2100, FH2140, CX140, FH2054, FH2062, FH2096, FH2001, FH2137, FH2159—Francisco et al. 1996; L. Francisco, pers. comm.; Ostrander et al. 1993). The amplification profile was 95°C for 5 min; 35 cycles of 95°C for 30 s, annealing temperature for 30 s, 72°C for 30 s; followed by 5 min at 72°C. Amplification products were stored in the dark at 4° or −20°C until analysis. Amplification products were electrophoresed in 3 multiplex sets, with an internal size standard (HD400-ROX, Applied Biosystems), through 6% Long Ranger gels (BioWhittaker Molecular Applications, Rockland, Maine) on an automated DNA sequencer (ABI Prism 377, Applied Biosystems). Analysis of amplification products was performed using Genescan (ver.3.2.1) and Genotyper (ver. 2.5) software (Applied Biosystems).

Statistical analyses.—We could not accurately estimate year of birth for all coyotes due to error rates associated with age estimates from cementum annuli (Gipson et al. 2000). Therefore, animals were grouped and analyzed 2 separate ways, using the November 1995 shift from nonselective to selective removal as the dividing point. First, we compared coyotes born through 1995 (n = 54) with those born after 1995 (n = 34). Coyotes were excluded if there was any ambiguity whether their year of birth was before or after 1995 or if they dispersed from HREC. Second, to examine impacts of removal strategy on different resident classes, radiocollared individuals were categorized at time of death as residents or transients, on the basis of observed reproductive status and movement patterns (Blejwas et al. 2002). Residents were affiliated with a single territory, whereas transients ranged over multiple territories. Almost all residents (33/38) were members of a mated pair (Blejwas et al. 2002). Group A comprised residents through 1995 (n = 15, 7 males, 8 females), group B was made up of transients after 1995 (n = 22, 9 males, 13 females), and group C was made up of residents after 1995 (n = 23, 10 males, 13 females). We had insufficient samples of known transients before 1995 for this type of analysis.

Forty-four coyotes were analyzed both by year of birth and by residence status. An additional 44 coyotes were included only in analysis by year of birth (n = 88), and an additional 16 coyotes were included only in analysis by residence status (n = 60).

For each group, heterozygosities, number of alleles per locus, global F_{is}, and unique alleles were determined using the Genetic Data Analysis software program (GDA—Lewis and Zay-

kin 2001, http://lewis.eeb.uconn.edu/lewishome/software.html). Deviations from Hardy–Weinberg equilibrium and linkage disequilibrium were calculated with GDA using exact tests, and a matrix of distance based on coancestry was generated. Estimates of F_{st} and significance based on bootstrapping also were calculated in GDA. Although *F* statistics were developed for spatial populations, we used them for comparative purposes. Allele frequencies at each locus were determined, and single locus and overall genetic differentiation were estimated using Fisher's exact test (Genepop ver.3.2a—updated version of the software in Raymond and Rousset 1995). Sequential Bonferroni adjustments (Rice 1989) were used to correct for multiple comparisons. The relatedness coefficient, *r*, for pairs of individuals and average *r* for groups were calculated using the program Relatedness 5.0 (Queller and Goodnight 1989). Six known sibling pairs and 6 known parent–offspring pairs were used to calculate average *r* of 1st-order relatives. Pairs of individuals with *r* within 1 *SD* of these known pairs (0.33–0.53) were considered putative 1st-order relatives. Values are presented as mean ± *SD*.

Results

We detected 102 alleles over all loci and sampling periods, and the total number of alleles per locus ranged from 4 to 19. Tables of allele frequencies by group are available on request. Mean expected single locus heterozygosities (H_e) over any sampling period ranged from 0.617 (FH2010) to 0.915 (FH2159), and observed single locus heterozygosities (H_o) ranged from 0.391 (FH2010) to 0.950 (FH2159).

Results for the analyses of coyotes grouped by year of birth are as follows. Number of alleles per locus detected within a group ranged from 4 to 16 and the average number of alleles per locus was 8.6 in coyotes born through 1995 and 7.7 in coyotes born after 1995. No departures from Hardy–Weinberg expectations were detected for either group. Significant linkage disequilibrium was detected between FH2137 and FH2159 for both groups. Values for single-locus H_e ranged from 0.617 to 0.887, and average multilocus H_e values were the same for both groups (0.76). Values for single-locus H_o closely agreed with expected values, and average values for multilocus H_o also were the same for both groups (0.76). Coyotes born through 1995 possessed 13 unique alleles at 6 loci, and those born after 1995 possessed 4 unique alleles at 3 loci. Global values of F_{is} were positive but small for both groups (0.004 through 1995, 0.007 after 1995) and, with a lack of excess homozygotes, indicated random mating within groups. Pairwise genetic distances between sampling periods were small (0.002), and overall multilocus F_{st} values between groups were not significantly different from 0, with the largest single-locus value being 0.011 (at both FH2010 and FH2140). An overall significant difference in allele frequencies was detected between groups ($P = 0.02$) due to a significant difference in allele frequencies at FH2140 ($P = 0.002$), in turn due to the presence of 5 low-frequency alleles in the group born through 1995 that were absent in those born after 1995. For the 88 individuals, average *r* was -0.012 ± 0.0039. For 6 known sibling pairs and 6 known parent–offspring pairs, average *r* was 0.41 ± 0.10 and 0.44 ± 0.11, respectively. Average *r* between individuals born through 1995 was -0.009 ± 0.004, and for individuals born after 1995 average *r* was -0.015 ± 0.004. Excluding known relatives, the average number of 1st-order relatives within groups was 1.65 ± 1.56 through 1995 and 1.24 ± 0.99 after 1995.

Results for the analyses of coyotes grouped by residence status are as follows. Numbers of alleles per locus detected within any group ranged from 4 to 13, and average numbers of alleles per locus were 6.8 (group A), 7.5 (group B), and 7.3 (group C). Significant departures from Hardy–Weinberg expectations were detected only at FH2010 in group C, and significant linkage disequilibrium was noted between FH2010 and 3 other loci in group C (FH2100, FH2140, and CX140). Values for single-locus H_e ranged from 0.627 to 0.915.

Values for average multilocus H_e were similar over groups: 0.770 (group A), 0.774 (group B), and 0.761 (group C). Values for single-locus H_o closely agreed with expected values for all 3 groups at most loci, and values for average multilocus H_o were 0.78 (group A), 0.742 (group B), and 0.724 (group C). One unique allele was detected in group A, 6 unique alleles were detected in group B (over 4 loci), and 5 unique alleles in group C (over 3 loci). Global values of F_{is} were negative for group A (-0.018) but positive for groups B (0.043) and C (0.050). A slight excess of homozygotes also was detected in groups B and C ($H_e > H_o$). The overall multilocus F_{st} among samplings was not different from 0, with the largest single-locus value being 0.015 (CX140). All pairwise multilocus values of F_{st} were indistinguishable from 0, and all pairwise genetic distances were 0. Following sequential Bonferroni adjustments, no significant single- or multilocus pairwise differences in allele frequencies were detected. Over all 60 individuals, average $r = -0.018 \pm 0.003$. Average r within groups A, B, and C was -0.023 ± 0.003, -0.016 ± 0.003, and -0.015 ± 0.003, respectively. Average numbers of 1st-order relatives within groups were low and ranged from 0.27 ± 0.45 (group A) to 1.00 ± 0.19 (group B).

Discussion

The HREC coyotes exhibit stable levels of microsatellite variation between periods of nonselective and selective removal. There was a higher level of removal of coyotes from the study site during the nonselective removal period of the study ($\bar{X}$ = 23.2 coyotes/year) than during the selective removal period ($\bar{X}$ = 6.2 coyotes/year—Blejwas et al. 2002). However, although changes in alleles and allele frequencies were detected over time, little fluctuation in levels of variation (e.g., average numbers of alleles per locus and multilocus heterozygosity) was observed, and little genetic structuring was detected at 11 microsatellite loci among temporal samples.

Although rare alleles at 1 locus caused differences in allele frequencies between groups by year of birth, random mating was indicated within both groups, and little genetic structure was detected between groups. Almost 1 additional allele per locus, on average, and 3 times as many unique alleles were detected prior to 1995 as after, possibly suggesting greater allelic diversity existed in coyotes born during nonselective removal. However, those values also could be influenced by sampling error. The average number of 1st-order relatives within groups was small and similar. Small and negative overall values for average r for both groups indicate low average relatedness within groups and little change in average relatedness between groups born during periods of different control tactics.

Analysis by residence status suggested a slight increase in inbreeding in both residents and transients, coinciding with the switch in removal tactics in 1995. Limited inbreeding also has been reported in other coyote populations (Roy et al. 1994). Average numbers of 1st-order relatives within all groups were low, and there was no increase in 1st-order relatives within groups after 1995 to account for that inbreeding. One explanation is a concomitant increase in half-siblings in the population (as lost mates are replaced by immigrants), increasing the likelihood of inbreeding (if inbreeding avoidance was less pronounced between half- than full-siblings). Relatedness analysis revealed many potential half-siblings (e.g., $0.1 < r < 0.3$) within groups (not shown). Immigration also could account for unique alleles detected after 1995. For example, 5 coyotes possessing 8 unique alleles originally were classified as transients but subsequently became resident breeders. Genetic heterogeneity could be limited among groups due to the presence of related coyotes in both resident classes, and pairwise comparisons indicated 1st-order rela-

tives between resident classes (not shown). Related animals belonging to both resident classes, as well as the movement of individual animals between resident classes, probably contributed to the finding of no significant genetic differences between classes or between residents under different removal regimes.

Although unique alleles were detected in all 3 groups by status, there are interesting implications of alleles detected only in transients. The lack of those alleles in any HREC breeders indicates that the 32% of transients possessing unique alleles are probably immigrants and may suggest some spatial genetic structure. Presumably unique alleles found in transients enter the local breeding pool if the transients establish territories and become successful breeders. Additionally, there were 19 alleles that only were detected after 1995, implying those alleles were present only in non-HREC breeders prior to 1995 and were contributed by immigrants. Many population-genetics studies use samples collected over time from a site, with little mention of temporal variation. These data demonstrate that even for panmictic populations some temporal genetic variation can exist within a site and that nonbreeders may act as a ''reservoir'' for allelic diversity.

Genetic stability between periods of nonselective and selective removal appears to reflect overall stability in the effective population size despite differences between those removal efforts. Nonselective removal disproportionately impacted the nonbreeding segment of the population (Sacks et al. 1999a), but elimination of nonbreeders from the population appears to have no greater local genetic impact than their dispersal would have. Although primarily breeding coyotes were removed during selective removal (Blejwas et al. 2002), gene dynamics under selective removal were apparently similar to those during nonselective removal, presumably due to the fact that the HREC population experienced relatively high genetic exchange with a larger, regional population. The ultimate result was temporal genetic stability of the local population during high individual turnover, despite differences in removal method.

The size of the management unit may influence any genetic impacts of removal efforts. For populations exploited over either small or large areas, recruitment of immigrants will occur. But populations exploited over larger areas may, in addition, have greater recruitment of locally bred juveniles than that of those exploited over a small area (Knowlton et al. 1999). Kin effects can impact genetic structure of local populations (Packer and Pusey 1982). In large management units, if offspring of current breeders move into territories and begin to breed alongside, or with, relatives as has been suggested in other coyote populations (Gese et al. 1996), the expectation could be locally structured populations, exhibiting inbreeding and many 1st-order relatives. In small managed units, in contrast, if vacant territories are claimed by random dispersers (e.g., transient coyotes), the expectation would be maintenance of genetic variation over time, limited inbreeding, and few 1st-order relatives. This 2nd explanation is more consistent with results from HREC. Additionally, under heavy exploitation, the removal rate may be so great that normal population dynamics are interrupted. It is possible that in a management unit larger than HREC or at removal rates lower than those at HREC, some degree of local structure will be detected.

Coyotes are exploited across their range, often with high percentages of local populations removed annually. Further, because coyotes are often controlled to reduce predation on livestock, as at HREC, populations that are under lethal management regimes tend to remain under those lethal regimes for extended periods of time. Although coyote population numbers seem to recover rapidly from these control efforts, the genetic consequences have not previously been explored. Despite limited inbreeding within resident groups after the

switch to selective removal, and behavioral and genetic evidence that some offspring of residents became residents on site (not shown), replacement of breeders appears to occur randomly from a large population, not from a single genetic source, implying that the localized removal effort does not negatively impact effective population size, irrespective of removal strategy. This suggests that, in the absence of physical barriers to movement and dispersal, individuals lost from HREC will continue to be replaced by recruitment from the much larger population of which it is a part. In a related work, we are examining the origin of replacements and dispersal patterns in this population in greater detail.

Territory size was relatively small at HREC, implying relatively high territory density and overall population density, with shorter replacement times than in areas of lower density (Blejwas et al. 2002). Stable genetic variation over 9 years in an exploited raccoon population (*Procyon lotor*—White et al. 1998) also was attributed to relatively large population size and low genetic drift. Removal strategies in that population were consistent from year to year but included both juveniles and breeding adults (White et al. 1998). On a shorter time scale, White and Svendsen (1990) also reported no genetic structuring over 2 years in a chipmunk (*Tamias striatus*) population, which they attributed to large effective population sizes. In contrast, temporal genetic variation has been reported in wildlife populations with small effective sizes (Zimmerman 1988) or experiencing large demographic changes or selective pressures (Scribner et al. 1983).

In a relatively small geographic population experiencing locally aggressive removal, coyote social structure and dispersal patterns appear to adequately maintain genetic variation and promote temporal genetic homogeneity. Comparisons with levels of temporal genetic variation in nonexploited populations as well as larger exploited populations are warranted.

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