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Social and genetic structure associated with migration in pronghorn

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ABSTRACT

Individual behavior promotes genetic structure within many mammalian populations, yet few studies have explored coarse- and fine-scale structure associated with migration. Fewer still have considered the conservation implications of such structure in at-risk populations. Pronghorn (*Antilocapra americana*) inhabiting Yellowstone National Park are partially migratory, and strong adult fidelity to migratory strategy and breeding areas may promote social and genetic structure within this population. We used 18 nuclear DNA microsatellite loci and fecal samples from 47 individuals to quantify group divergence and pairwise relatedness of Yellowstone pronghorn. The genetics of this population are characterized by individual isolation by distance ($P = 0.009$). Evidence for fine-scale social and genetic structure was strong, with mean relatedness between individuals declining rapidly with geographic distance (0–3 km) within areas selected by both migrants and non-migrants. On average, females sampled within social groups were related at the level of first cousins (mean $R = 0.105 \pm 0.192$ SD). We found low differentiation of the population by migratory strategy ($F_{ST} = 0.019$), moderate differentiation among some summer use areas ($F_{ST} \geqslant 0.033$), and an excess of heterozygotes within all migrant groups ($F_{IS} \leqslant -0.017$). Weak and inconsistent substructure was detected using spatial and aspatial Bayesian clustering methods. Our results are the first to document fine-scale social and genetic structure in pronghorn, most likely organized along matrilines. Access to a majority of the total summer range available to this population is maintained by social inheritance and individual fidelity to areas of use. The maintenance and reestablishment of migratory routes may therefore hinge on the retention of experienced individuals, the strength of natal and adult philopatry, and the accessibility of seasonal habitat to pioneering females.

1. Introduction

Many mammalian populations are genetically structured at both coarse and fine scales due to male-biased dispersal, female philopatry, and/or polygynous mating systems (Chesser, 1991, 1998; Storz, 1999). Another factor that may increase genetic structure in some populations is seasonal migratory behavior (Chapman et al., 2011; Mathews and Porter, 1993; Nelson and Mech, 1987). Migration inherently structures populations spatiotemporally. For species with male-biased dispersal and female philopatry to seasonally-restricted habitats (Clutton-Brock, 1989; Greenwood, 1980), migratory females are disproportionately replaced by migratory daughters over time, reinforcing genetic structure as well (Tiedemann et al., 2000). This effect may be maximized within partially migratory populations (those in which some but not all individuals migrate) characterized by substantial reproductive isolation of migrants during the breeding season (Wright, 1943).

A consequence of genetic divergence within partially migratory populations, however, may be dependence upon an increasingly-related subset of individuals to facilitate critical access to habitat (Alerstam et al., 2003; Fryxell and Sinclair, 1988). For example, mortality or population removals which impact migrants may inadvertently lead to route abandonment for generations (Craighead et al., 1972; Stevens and Goodson, 1993). The sudden reduction in total habitat availability may imperil populations in which reproductive success by migrants contributes significantly to overall recruitment (Allendorf et al., 2008; Bolger et al., 2008). Similarly, inbreeding depression within a portion of the population could reduce the resilience of the overall population to stochastic winter severity, habitat loss elsewhere within the population's range, or other environmental stressors.

Scott (1990) hypothesized that non-migrant and migrant pronghorn (*Antilocapra americana*) inhabiting the northern portion of Yellowstone National Park (YNP), an historic population at-risk of extirpation due to high fawn mortality and winter range

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degradation (Barnowe-Meyer et al., 2009; Boccadori et al., 2008; National Research Council, 2002), constitute genetically distinct groups that should be managed as distinct conservation units (Moritz, 1994). Genetic evidence for kin-based sociality and population structure in pronghorn is weak (Byers, 1997; Pyrah, 1987). However, behavioral data indicate relatively strong fidelity of adult females to migratory strategy and summer use areas in this population White et al. (2007b), suggesting that kin association could promote divergence of the Yellowstone pronghorn population by migratory strategy. Yellowstone pronghorn are maximally distributed across a relatively linear and narrow 60 km range from spring through the autumn breeding period, increasing the potential for localized, non-random mating with distance traveled from the winter range (Wright, 1943). Additionally, the presence of genetic subgroups within this population may provide an explanation for historic range abandonment within some interior areas of YNP following population culls in the 1940s (Keating, 2002), underscore potential adverse effects of future infrastructure developments within migration corridors and seasonal range areas (Caslick, 1998; Scott, 1992), and highlight strategies to facilitate the renewed use of abandoned habitat (Gustafson and Gardner, 1996; Piper, 2011).

To investigate relationships among kin association, migratory fidelity, and genetic structure in the YNP pronghorn population, we assessed patterns of relatedness and differentiation within migratory and non-migratory portions of the population. Our objectives were to assess evidence for coarse- and fine-scale genetic structure associated with migratory status and areas of summer use, test for the presence of cryptic genetic subgroups within the population, and interpret our results in the context of historic range abandonment within Yellowstone National Park.

2. Methods

2.1. Study area

Yellowstone pronghorn occupy approximately 330 km^2 of Yellowstone National Park's northern range in Montana and Wyoming, USA (Fig. 1). Elevations of habitual use areas range from 1500 m to 3000 m. During winter, pronghorn occupy an arid and windswept basin of approximately 30 km^2 near Gardiner, Montana (Boccadori et al., 2008). Beginning in April of each year, a portion of the population migrates to a series of discrete meadow complexes and high-elevation ridges within YNP where birthing, fawn-rearing, and breeding occur (White et al., 2007b). Pronghorn are distributed non-continuously across their range during this period. Migrating individuals return to the winter range between September and October of each year. Non-migrant individuals occupy the winter range year-round (White et al., 2007b). Most individuals remain consistent in their migratory strategy across years (White et al., 2007b). During the period of this study, the Yellowstone pronghorn population numbered approximately 300 individuals (National Park Service, unpublished data).

2.2. Field sampling and microsatellite genotyping

Genetic sampling occurred from late June through August 2006 when female movements among areas were minimal (White et al., 2007b) and fawning was complete (Barnowe-Meyer et al., 2011). We collected naturally deposited fecal samples from undisturbed pronghorn. Only adult female samples, determined based upon visual observations of defecation events, were used for analyses. Samples were obtained in the following areas of northern Yellowstone: the Gardiner Basin (winter range), Blacktail Deer Plateau, Specimen Ridge, Lower Lamar Valley, and Upper Lamar Valley (Fig. 1). We placed samples in sanitized plastic bags within one hour of defecation and transferred bags to a freezer within 8 h of collection. We recorded Universal Transverse Mercator coordinates (zone 12 N) using a handheld Garmin eTrex GPS unit (Garmin Ltd., Olathe, Kansas).

We extracted DNA from fecal samples in the Laboratory for Ecological, Evolutionary, and Conservation Genetics (University of Idaho, Moscow ID) in a room dedicated to low-quantity DNA sources. We employed the materials and protocols provided by the QIAamp DNA Stool Mini Kit (QIAGEN Inc., Valencia CA) with modification: target cells on the outer surface of the pellet were washed free for analysis using Buffer ASL rather than extracted from the entire homogenized pellet (Wehausen et al., 2004). Analyses were conducted using 18 microsatellite loci: *Aam1-2, Aam4-7,* and *Aam9-18* (GenBank accession numbers AF525012-AF525013, AF525015-AF525018, and GU289706-GU289715, respectively; Carling et al., 2003; Dunn et al., 2010); *ADCYC* (Lou, 1998); and *PrM6506* (Stephen et al., 2005). We amplified DNA fragments using polymerase chain reaction (PCR) with volumes and a thermocycler touchdown profile specific to pronghorn fecal samples (Dunn et al., 2010). We visualized PCR products using an ABI Prism 3130xl capillary system and scored the alleles using program GENEMAPPER version 3.7 (Applied Biosystems, Foster City CA). We included negative controls during the extraction and PCR processes to monitor for contamination. We determined consensus genotypes based on 3–6 PCR replicates per sample. We accepted genotypes if alleles were observed 3 times in the case of homozygotes and at least 2 times each in the case of heterozygotes. We then verified consensus genotypes using the consensus genotype function of GIMLET version 1.3.3 (Valiere, 2002). We assessed probability of sample identity and probability of identifying siblings (Waits et al., 2001) using GIMLET, removing duplicate samples (from the same individual) as appropriate. After removal of poor quality and duplicate samples, we retained 14 samples (Gardiner Basin) from non-migrant individuals and 33 samples from migrant individuals including 2 from the Blacktail Deer Plateau, 9 from the Lower Lamar Valley, 10 from Specimen Ridge, and 12 from the Upper Lamar Valley (Fig. 1). We dropped the Blacktail Plateau individuals from analyses involving spatial differentiation (except in a migrant versus non-migrant analysis) due to a low sample size.

2.3. Analyses

We used programs STRUCTURE version 2.0 (Falush et al., 2003; Pritchard et al., 2000), TESS version 2.3 (Chen et al., 2007; Durand et al., 2009), GENELAND (Guillot et al., 2005; Guillot et al., 2008), FLOCK version 2.0 (Duchesne and Turgeon, 2012), and Principle Components Analysis (PCA) to assess coarse-scale genetic structure within the Yellowstone pronghorn population. We used Nei's genetic distance between individuals (Nei and Roychoudhury, 1974) and standardized as well as non-standardized covariance and distance matrices during PCAs in program GenAlEx version 6.5 (Peakall and Smouse, 2012).

In program STRUCTURE, we used a burn-in period of 10,000 Markov chain Monte Carlo (MCMC) iterations and 100,000 MCMC repetitions, an admixture ancestry model, and a correlated allele frequency model (Pritchard et al., 2000). Inference was based upon 10 iterations for each value of K from 2 to 10 using program STRUCTURE HARVESTER version 0.6.92 (Earl and von Holdt, 2012; Evanno et al., 2005). We examined individual assignments and probabilities from the highest likelihood run under the best-supported value of K.

In program TESS, we used a burn-in period of 10,000 MCMC iterations, 100,000 MCMC repetitions, and an admixture ancestry model based upon both conditional auto-regressive (CAR) and convolution (BYM) Gaussian models (detailed in Durand et al., 2009).