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Conservation genetics of managed ungulate populations

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Natural populations of many species are increasingly impacted by human activities. Perturbations are particularly pronunced for large ungulates due in part to sport and commercial harvest, to reductions and fragmentation of native habitat, and as the result of reintroductions. These perturbations affect population size, sex and age composition, and population breeding structure, and as a consequence affect the levels and partitioning of genetic variation. Three case histories highlighting long-term ecological genetic research on mule deer *Odocoileus hemionus* (Rafinesque, 1817), white-tailed deer *O. virginianus* (Zimmermann, 1780), and Alpine ibex *Capra i. ibex* Linnaeus, 1758 are presented. Joint examinations of population ecological and genetic data from several populations of each species reveal: (1) that populations are not in genetic equilibrium, but that allele frequencies and heterozygosity change dramatically over time and among cohorts produced in successive years, (2) populations are genetically structured over short and large geographic distances reflecting local breeding structure and patterns of gene flow, respectively; however, this structure is quite dynamic over time, due in part to population exploitation, and (3) restocking programs are often undertaken with small numbers of founding individuals resulting in dramatic declines in levels of genetic variability and increasing levels of genetic differentiation among populations due to genetic drift. Genetic characteristics have and will continue to provide valuable indirect sources of information relating enviromental and human perturbations to changes in population processes.

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Introduction

There is a practical need in biological conservation for understanding the effects of environmental and human perturbations on demographic and genetic characteristics of natural populations. Species have presumably evolved intrinsic mechanisms to cope with temporal variation in environmental characteristics. However, in recent times populations of many if not most species are increasingly subject to further perturbations due to human activities. For example, habitat loss and fragmentation may result in localized extinctions (Wilcox 1980). Gene flow among remaining habitat patches may be severely reduced resulting in lower effective population size, loss of genetic variability, and possible increased levels

of inbreeding (Lande 1988). Numerous species are harvested commercially or for sport. Such exploitations may severely reduce population numbers and are often directed toward specific sexes and age/size cohorts. Harvests may also dramatically reduce effective population numbers (Ryman *et al.* 1981) and may change population breeding structure (Scribner *et al.* 1985). Finally, many species have been targeted for translocations in attempts to locally increase population size, to establish species in vacant habitats, or to reintroduce species in historically occupied ranges. Reintroduced populations are often established with relatively few individuals of unknown genetic relationship. Such populations may be particularly susceptible to loss of genetic variation due to inbreeding and genetic drift (Stüwe and Scribner 1989, Leberg 1990, Stüwe *et al.* 1992). Each of the manipulative changes outlined above may exert additional pressures on local populations to the point where they cease to be capable of responding demographically and genetically to changing conditions via naturally evolved deterministic processes and are increasingly susceptible to stochastic events.

Large mammals may be particularly susceptible to environmental and human influences. Such species are typically long-lived, have long generation times, and comparatively low habitat specificity. Many species of ungulates are characterized by polygonous mating systems which reduce effective poulation size. Populations of large mammals may also be particularly subject to the negative affects associated with prolonged bottlenecks due to relatively low natality.

Estimates of levels of genetic variability within populations and of the magnitude of genetic variation among populations have frequently been used to make inferences about present and historical pròcesses affecting natural populations (Nevo *et al.* 1984). Managers and conservation professional have become increasingly aware of the utility of population genetic data in assessing population viability and in the esablishment of management objectives. To be effective, management strategies should be tailored to individual species or populations and should incorporate information of species-specific ecological characteristics and the degree to which these characteristics may vary temporally under "natural conditions". Unfortunately, few data exist where both genetic and demographic characteristics have been monitored jointly over extended periods of time.

Data described in this presentation highlight portions of several extensive long-term ecological genetic studies of large mammalian species. Three case histories are presented which describe and compare genetic characteristics for mule deer *Odocoileus hemionus* (Rafinesque, 1817), white-tailed deer *Odocoileus virginianus* (Zimmermann, 1780), and Alpine ibex *Capra ibex ibex* Linnaeus, 1758. Our general goal was to document the degree of spatial genetic structuring among groups of each species, to determine the temporal resilience of this spatial structure if present, and attempt to define agents responsible for the magnitude and transiency of this structure over time.

Methods

Data were obtained from free ranging populations of each species. Species differ greatly in population ecology, in movement patterns, and in habitat specifity; intrinsic properties which influence species (and population) susceptibility to enviromental and human factors, and which determine the degree to which genetic variation is partitioned within and among populations. Interpretation of genetic data has been greatly enhanced by the excellent background demographic and ecological characteristics which were collected concurrently.

Mule deer

Background: Data were collected from large migratory herd (n = 16,000 – 27,000 during the period of study; Colorado Division of Wildlife, unpubl. data) which winter in the Piceance Basin (approx. 1,722 km^2) in northwestern Colorado, USA. The herd may be divided into a northern and southern subdivision based on seasonal migratory patterns. Deer which winter in the northern portion of the Piceance Basin migrate to summer ranges to the northeast, while deer which winter in southern areas of the basin migrate to the south and southeast. During the winter deer are primarily found in matriarchal groups composed of one or several adult females, yearling females, and fawns. Despite their seasonal migratory habits matriarchal groups are highly philopatric to specific winter areas within the basin and will remain within a small area throughout the winter unless high snow fall necessitates movement into lower elevations. Researchers using tag return data (Bartman and Stewart 1981) and radio telemetry (Garrott *et al.* 1987) have shown that there is little movement of individuals between northern and southern subdivisions.

The Piceance herd is heavily impacted by enviromental factors (primarily winter severity) and by sport harvest. Recruitment rates are high (fawns annually comprise approximately 25% of the fall population). However, fawn overwinter mortality is extremely variable from year to year. Mortality rates may be quite high, exceeding 94% in some years (White *et al.* 1987). In addition, year to year variation in weather conditions may affect the timing of reproduction and juxtaposition of animals during the breeding season (R. A. Garrot, pers. comm.). Herd sex ratios are highly skewed in favor of females (adult sex ratio approx. 20 females : 1 male; Colorado Division of Wildlife, unpubl. data) due principally to male only sport harvest.

Data analysis: Electrophoretic analyses were conducted using blood taken from live-trapped adult and yearling females and fawns (n = 681) over four consecutive years (1983 – 1986). Five to 10cc of blood was obtained from jugular vein of each individual using a heparinized vacutainer. Blood was stored on wet ice in the field. Samples were subsequently centrifuged and plasma and hemolyzed erythrocyte fractions were separated and stored in liquid nitrogen. Twenty five protein loci were revealed using horizontal starch-gel electrophoresis. Buffer systems and loci resolved are described in detail in Scribner *et al.* (1991). Allele frequencies and estimates of multi-locus heterozygosity were calculated for adult females and fawns for each of the four years. Differences between age classes and years were quantified using a categorical model analog of an analysis of variance (Grizzle *et al.* 1969). The degree of spatial genetic structuring was assessed using contiguous cluster analysis (Chesser and van den Bussche 1988) using counts of the number of individuals of specific genotype at the 6-*Pgd* locus for each of 25 locations where live-trapping was conducted. In brief, the contiguous clustering technique tests for the presence of non-random contiguous associations of individuals of the same genotype using hyper geometric sampling probabilities. Trap locations were further used in the calculation of F-statistics (Wright 1965, Nei and Chesser 1983). The sign and magnitude of one component of this analysis (F_{IS}) was used as a measure of departure from random mating (i.e. as an indicator of excess ($-F_{IS}$) or deficiency ($+F_{IS}$) in the number of heterozygous individuals associated with each trap location).

White-tailed deer

Background: Due to over-harvest and poaching, white-tailed deer were extirpated from much of their original range in the southeastern United States by the mid-1900's. After enactment of strict harvest regulations, populations expanded rapidly from remnant populations as the result of extensive reintroduction programs. White-tailed deer on the Department of Energy's Savannah River Site (SRS) were thought to have expanded from a small population inhabiting inaccessible areas immediately adjacent to the Savannah River. The SRS population was protected from the early 1950's until 1965 when controlled hunts were established to control population numbers.

Approximately 25% of the herd is harvested during each year (Novak *et al.* 1991) by either of two hunting methodologies. Dog hunting was used in most areas during 1965 – 1988. From 1969 through 1980 certain areas were subjected to only still hunting. These still-hunted regions were subsequently subjected to dog hunting only (from 1980 to present). Detailed descriptions of harvest methodology, and the effects on herd population size, demographic composition, and genetics can be found in Scribner *et al.* (1985) and Novak *et al.* (1991). Genetic data has been taken continuously over the period 1973 – 1988.

Data analysis: We were primarily interested in assessing the degree to which this herd was spatially genetically structured and if this structure changed over time. The entire SRS was divided into 4 km^2 grids and all deer harvested during each year were assigned to an *x-y* grid coordinate. Sex, age and body size were recorded for each individual. Blood and liver samples were also taken from each deer and used for allozyme electropheresis. Data for beta-hemoglobin (*ß-Hb*) and sorbital dehydrogenase (SDH) for the years 1974 – 1982 were used in analyses.

Contiguous cluster analysis (Chesser and van den Bussche 1988) was used to determine the degree of non-random genetic structure during the years 1974 – 1977. Analyses were conducted using counts of single-locus genotypes at the *Sdh* locus from each 4 km^2 grid. Analyses addressing the effects of harvest methodology on temporal variation in allele frequency were conducted using data from individuals harvested in regions of the SRS subjected to either still- or dog-hunting. Allele frequencies at the *ß-Hb* locus were calculated for deer harvested during each year in each region. Significance of year to year changes in fawn allele frequency within each area was assessed using contingency χ^2-square analysis (Sokal and Rohlf 1981).

Alpine ibex

Background: Alpine ibex once occupied mountainous regions across much of Europe. By the early 18th century ibex distribution was reduced to a single population in Gran Paradiso mountain massif in northwestern Italy. Declines in population size and in the number of populations was due to over harvest and to pouching, despite the enactment of drastic laws as early as 1523 (Ausserer 1946). The Gran Paradiso population has been protected by the Italian goverment since 1821. Population size increased dramatically and animals were subsequently used to establish additional populations in captive breeding facilities and in natural habitats. During the last 80 years ibex have been reintroduced into alpine habitats throughout much of their original range.

Alpine ibex are ideally suited to address questions regarding the effects of reintroductions on population levels of genetic variability and the rates and magnitude of genetic divergence among populations. Founding histories and per-generation population demographic characteristics are known for most populations. In addition, inter-population genetic differences are solely a function of founding histories and intrinsic population dynamics following each founding event. Ibex inhabit alpine habitat exclusively, and little if any gene flow occurs between populations from disjunct mountain habitats (Nievergelt 1966).

Data collection: We wished to determine the effects of founding population characteristics and post-introduction population dynamics on present levels of heterozygosity and to document the magnitude of genetic divergence among source and reintroduced populations. Blood or tissue samples were obtained from individuals (n = 415) from 23 populations in Italy, France, Switzerland and Germany.

Fifteen loci were consistently resolved for all individuals. Loci used for analyses include albumin, phosphoglucomutase-3, β-hemoglobin, glucose phosphate isomerase-1, creatine kinase-2, glucose-6--phosphate, malate dehydrogenase-1, 6-phosphogluconate dehydrogenase, malic enzyme-1, purine nucleoside phosphorylase, lactate dehydrogenase-1, eurythracytic acid phosphatase, peptidase-B and superoxide dismutase-1,2. Estimates of multi-locus heterozygosity were calculated for each population. Differences in heterozygosity among populations were determined using contigency χ^2 analysis. Pair-wise estimates of genetic variance among populations were quantified using F-statistics (Wright 1965). Inter-population variance estimates were compared for populations founded by stocking and by natural dispersal.

Relationships betwen current population estimates of heterozygosity and population demographic characteristics (founding effective population size, population growth rate and carrying capacity) were conducted using Spearman's rank-order correlation analysis. Data of founding population size, sex and age structure during each year following the introduction were obtained from wardens and biologists from each region. Effective population size was calculated for each generation (approx. 9 years; Stüwe and Grodinski 1987) as $4N_f N_m/(N_f + N_m)$ where N_f and N_m represent the number of adult females and males, respectively during each generation.

Results

Mule deer

Genetic characteristics of mule deer vary greatly both spatially within the Piceance Basin, and over time. Mule deer are not panmictic but exhibit significant genetic structure as seen by the non-random dispersion of genotypes among the

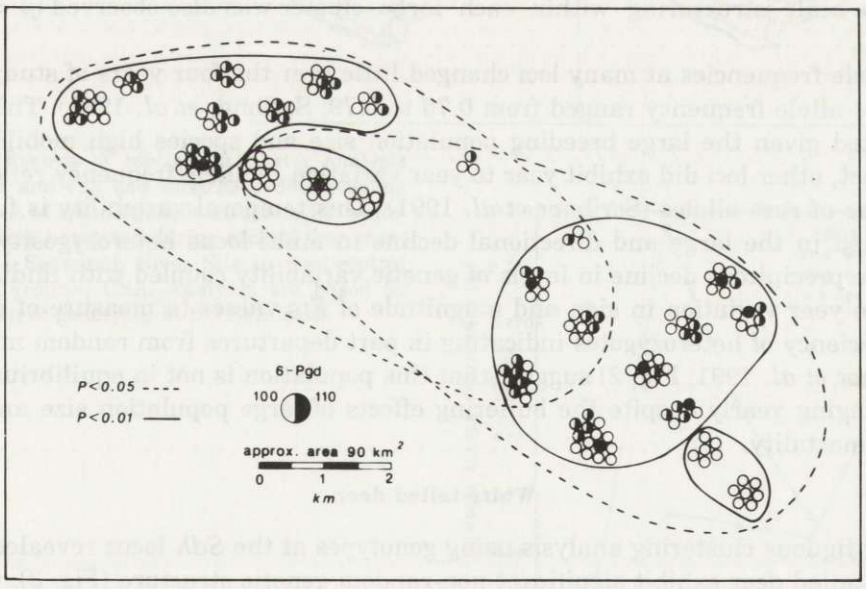

Fig. 1. Results of contiguous cluster analysis (Chesser and van den Bussche 1988) showing the extent of spatial genetic structure for mule deer captured from 24 trap locations in the northern region of the Piceance Basin, in northwestern Colorado, USA during 1986. Analyses are based on the dispersion of genotypes at the 6-*Pgd* locus.

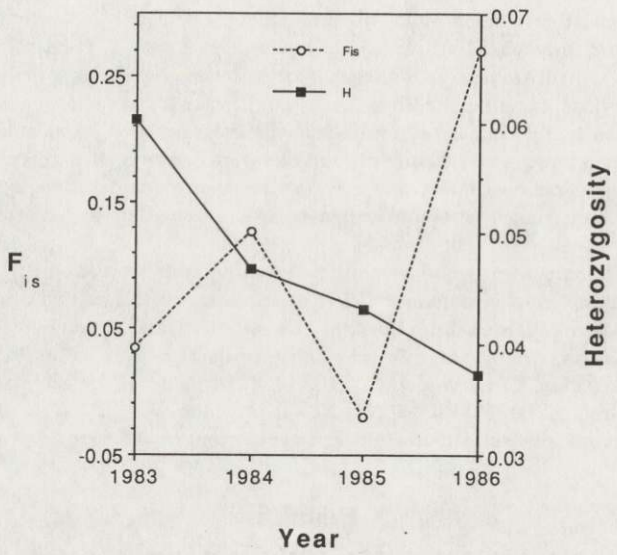

Fig. 2. Temporal changes in herd inbreeding coefficient (F_{IS}) and heterozygosity over the period 1983 – 1986. Data represent mean values over all polymorphic loci for all fawns and adult females captured from 20 trap locations in two wintering-herd subdivisions during each year.

capture locations within the northern migratory subdivision (Fig. 1). Contiguous cluster analysis reveal two large clusters of individuals ($p < 0.05$; Fig 1). Evidence of fine-scale structuring within each large cluster was also observed ($p < 0.01$; Fig. 1).

Allele frequencies at many loci changed little over the four years of study (e.g. *Pgd-64* allele frequency ranged from 0.76 to 0.79; Scribner *et al.* 1991). This was expected given the large breeding population size and species high mobility. In contrast, other loci did exhibit year to year variation in allele frequency reflecting the loss of rare alleles (Scribner *et al.* 1991). This temporal variability is further reflected in the large and directional decline in multi-locus heterozygosity (Fig. 2). The precipitous decline in levels of genetic variability coupled with findings of year-to year variation in sign and magnitude of F_{IS} values (a measure of excess or deficiency of heterozygotes indicating in part departures from random mating; Scribner *et al.* 1991; Fig. 2) suggest that this population is not in equilibrium but is changing yearly despite the buffering effects of large population size and low adult mortality.

White-tailed deer

Contiguous clustering analysis using genotypes at the *Sdh* locus revealed that white-tailed deer exhibit significant non-random genetic structure (Fig. 3). Genotypes of the 'M' allele were primarily clustered in the southern portion of the SRS while genotypes of the 'S' and 'F' allele were principally found in the central and northern areas; a pattern consisted with previous comparisons of individuals from

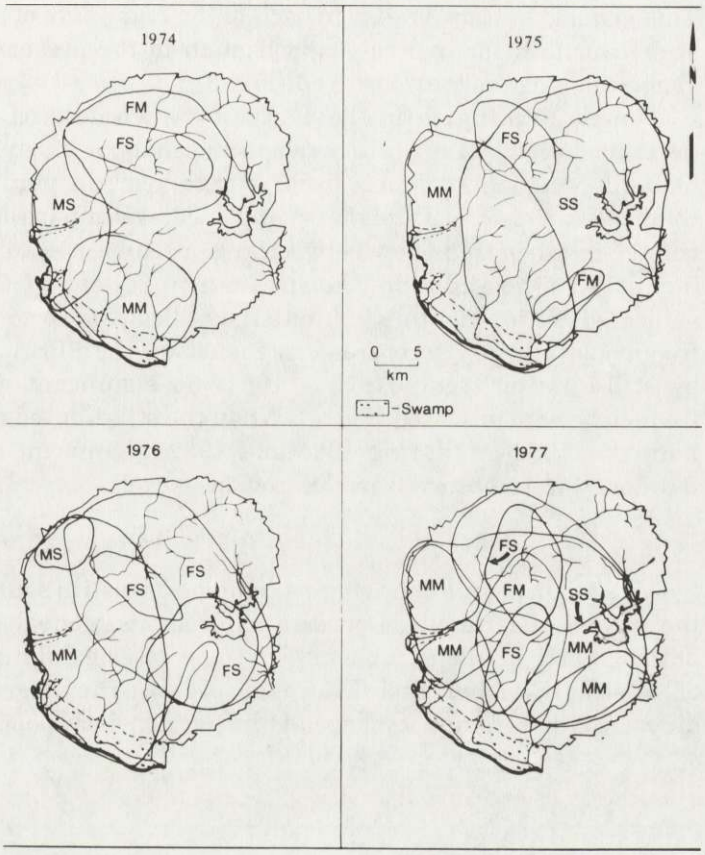

Fig. 3. Results of contiguous cluster analysis (Chesser and van den Bussche 1988) revealing the extent of spatial genetic structure for white-tailed deer harvested during each of four years from the Savannah River Site in west-central South Carolina, USA. Analyses are based on dispersion of genotypes at the *Sdh* locus.

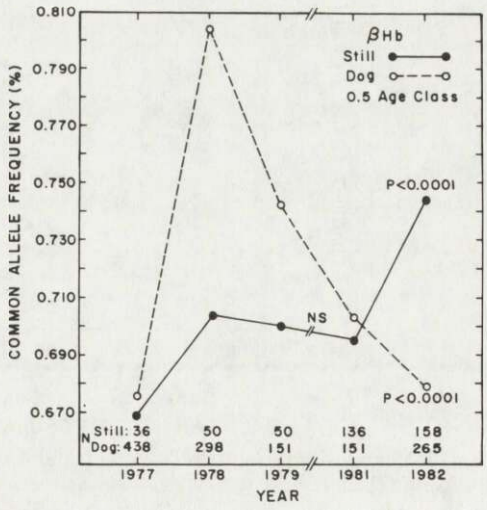

Fig. 4. Annual variation in *β-Hb* common allele frequency for fawns harvested from regions of the SRS subjected to either still- or dog-hunting.→

southern 'swamp' and northern 'upland' regions of the SRS (Ramsey *et al.* 1979). This general pattern is seen in each of the four years of study. However, on a finer scale considerable year to year variation in the presence and position of specific genotypic clusters was observed (Fig. 3).

Temporal variation in the degree to which deer on the SRS were structured (as determined by the position of specific gentypic clusters) may be due to changes in herd breeding structure from year to year; in part due to intensive harvest conditions. This hypothesis was supported by comparisons of the degree of annual change in allele frequency between regions subjected to different hunting regimes (i.e. still- vs dog-hunting). Fawns born in regions of the SRS where deer were subjected to dog hunting exhibited significant year to year differences in allele frequency (Fig. 4). In contrast, in regions of the SRS where deer were harvested by still-hunting (years 1977 – 1981) no significant differences in fawn allele frequency were observed (Fig. 4). When the still-hunted regions were subsequently hunted with dogs (during 1981 and 1982) significant differences in fawn allele frequency were observed in this region as well.

Alpine ibex

All 23 ibex populations share a common ancestral source (Gran Paradiso) within the past 8 generations. Despite their common genealogical history, populations differ greatly in allele frequency; in some cases exhibiting near alternate fixation of alleles (Scribner and Stüwe, in press). The degree to which populations differ in allele frequency depends in part on how populations were established.

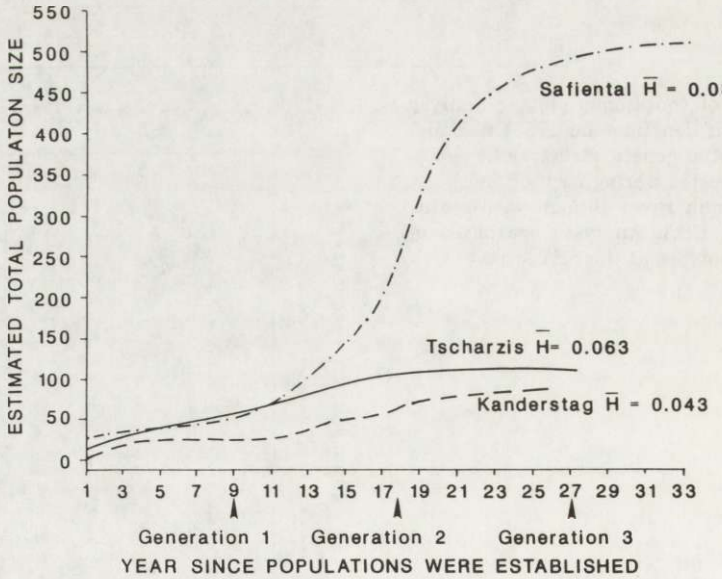

Fig. 5. Changes in population size and population heterozygosities for three reintroducted populations of Alpine ibex.

Populations established via natural dispersal differed from their source population to a smaller degree than did those populations founded by reintroductions (mean F_{ST} = 0.092 and 0.212, respectively; Table 1). No differences between dispersal and reintroduction founded populations were observed in levels of heterozygosity, proportion of polymorphic loci, or number of alleles per locus (Table 1). Further, Fixation indices for all populations were not significantly from zero suggesting that populations were in Hardy-Weinberg equilibrium.

Large differences in heterozygosity were observed among populations established by reintroductions (H range from 0.027 to 0.083; Table 1 and Fig. 5). Current levels of heterozygosity were correlated with population founding history and population demographic characteristics following establishment. A significant correlation was documented between population heterozygosity and the effective founding population size (Scribner and Stüwe, in press). Three populations established by reintroductions show the rank-order realtionship between founding numbers, population growth rates and heterozygosity. The Safiental population had the highest heterozygosity (0.083) and was established with the largest number of individuals and grew in numbers more rapidly that the Tscharzis (0.063) or Kanderstag (0.043) populations.

Discussion

By combining observations of species-specific genetic characteristics and population ecology this study addresses the importance of various human perturbations to spatial genetic relationships among populations and to changes in population genetic characteristic over time. Studies of populations of Alpine ibex, mule deer and white-tailed deer have revealed several major results. Firstly, within the regions under study, populations of each species were not panmictic but were spatially stuctured. The manner in which genetic variation was partitioned within and among populations differed greatly among species reflecting species-specific life histories and propensity for gene flow. Alpine ibex, which have historically been restricted to disjunct alpine habitats, and which have been repeatedly subject to bottlenecks in population numbers due to reintroductions, exhibited low heterozygosity and high interpopulation genetic divergence. In contrast, mule deer and white-tailed deer, which were more continuously distributed, exhibited high levels of heterozygosity and relatively low levels of spatial genetic structure. Mule deer and white-tailed deer were genetically structured on a fine geographic scale (Figs 1 and 3) reflecting matriarchal social structure and female site fidelity.

A second major finding revealed large year to year variation in genetic characteristics within populations. Temporal changes were observed in the degree and position of contiguous genetic associations (Fig. 3), in allele frequency (Fig. 4) and in inbreeding coefficients (F_{IS}; Fig. 2).

Directional declines in mule deer herd heterozygosity was unprecedented for a free-ranging vertebrate population. High male and female reproductive variance

resulting from high overwinter fawn mortality and highly skewed adult sex ratios have presumably contributed to the stochastic loss of rare alleles and heterozygosity decline. However, these factors alone can not account for the magnitude of decline in heterozygosity or loss of total genetic variance (K. T. Scribner and R. K. Chesser, in prep.). Selection must underlie a portion of observed changes and should be considered in future management plans.

Temporal changes in F_{IS} may reflect annual adjustments in timing of migratory movements. Year to year variation in migratory patterns could lead to annual differences in juxtaposition of adult males and females during the breeding season. Annual differences in population breeding structure would be reflected in the sign and magnitude of F_{IS}. Positive F_{IS} could result from inbreeding or from a high correlation of gametes among individuals within spatially segregated matriarchal groups (Scribner *et al.* 1991). Similarly, negative F_{IS} could indicate a reverse Wahlund effect caused by mating during times when the herd is not spatially structured (i.e. during migration).

In the case of white-tailed deer, the year-to-year variation in population genetic characteristics is largely the result of harvest practices. Hunting occurs during the breeding season. Hunting with dogs results in the large-scale movements of individuals which disrupts matriarchal groups and herd breeding structure. This leads to year-to-year variation in allele frequencies of fawns born the following year (Fig. 4) and to changes in position of contiguous genotypic associations within the SRS (Fig. 3). Managers have only recently become aware of the importance of inbreeding and the loss of genetic variability that can occur due to drift when establishing new populations. Historically large and outbreeding populations that suddenly decline in size to few individuals may experience declines in genetic diversity. In small populations, random fluctuations in gene frequency tend to lead to increased homozygosity and possible loss of evolutionary adaptability to future environmental changes (Allendorf and Leary 1986). Similarly, populations may experience reduced viability and fecundity due to inbreeding depression (Lande 1988). Reintroductions are often made with few individuals (usually without knowledge of genetic relationships). Comparisons of reintroduced Alpine ibex populations suggest that the manner in which reintroductions were conducted dramatically affected genetic characteristics of founded populations.

Low levels of heterozygosity documented for Alpine ibex reflect management actions rather than species-wide evolutionary histories. Heterozygosities of Alpine ibex were significantly lower than has been documented for another closely related subspecies (Nubian ibex *Capra ibex nubiana*; H = 0.047 and 0.087, respectively; Stüwe *et al.* 1992) which have not been subjected to repeated reductions in population size. Theoretical studies have shown that loss of heterozygosity is related to the severity and length of the population bottleneck (Chakraborty and Nei 1977). For Alpine ibex, population heterozygosity was significantly correlated to effective size of the founding populations (Fig. 5). Populations which were

Table 1. Genetic characteristics of Alpine ibex populations established by natural dispersal or by reintroductions. [a] means across all populations, [b] means pair-wise estimates of F_{ST} between populations, [c] means multi-locus heterozygosity across all populations based on 15 loci.

Genetic characteristics[a]	Population founding history	
	Natural dispersal (n = 2)	Reintroductions (n = 5)
Inter-population genetic divergence[b]	0.092 (0.083 to 0.101)	0.212 (0.087 to 0.347)
Fixation index (F)	−0.034 (−0.019 to −0.048)	−0.085 (−0.429 to 0.179)
Heterozygosity[c]	0.058 (0.038 to 0.077)	0.050 (0.027 to 0.066)
Proportion of loci polymorphic	11.6 (7.4 to 15.4)	13.9 (7.4 to 15.4)
Number of alleles per locus	1.20	1.20

founded with few number of individuals and whose size remained small for several generations (e.g. Tscharzis and Kanderstag; Fig. 5) had low heterozygosities.

Reintroductions of Alpine ibex have resulted in accelerated rates of genetic drift within newly founded populations. The degree of genetic divergence (i.e. F_{ST}) among founder and reintroduced populations was higher than that observed between populations founded by natural dispersal (Table 1). In many cases pair-wise estimates of observed and expected variance (under genetic drift given estimates of per generation effective population size) were very similar (Scribner and Stüwe, in press) suggesting that genetic drift and not selection account for much of the high inter-population divergence observed. Levels of genetic divergence among populations (Table 1) are much higher than have been documented among continental populations of other large mammals (e.g. red deer *Cervus elaphus* – Gyllensten *et al.* 1980, moose *Alces alces* – Ryman *et al.* 1980, and reindeer *Rangifer tarandus* – Roed 1985).

Conclusions

Frequently, insufficient attention is given to gathering or evaluating data on how intrinsic social factors and dispersal abilities affect the distribution of genetic variation within and among natural populations. In addition, few long-term studies have been conducted to determine the extend and cause of temporal changes in population demographic and genetic characteristics. These data clearly show that populations of large mammals are not in equilibrium but change dramatically from year to year. The extend of human perturbations varies from species to species. However, man has clearly affected the genetic characteristics of many large mammalian species. Genetic characteristics have and will continue to provide

valuable sources of inference. However, interpretations must be made in the context of species-species population ecology and natural propensities for change over short and long time periods.

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