

Carnivores in Ecosystems: The Yellowstone Experience

Edited by Tim W. Clark

A. Peyton Curlee

Steven C. Minta

Peter M. Kareiva

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Genetic Considerations for Carnivore Conservation in the Greater Yellowstone Ecosystem

F. Lance Craighead, Michael E. Gilpin, and Ernest R. Vyse

With the recent reintroduction of the gray wolf, the Greater Yellowstone Ecosystem (GYE) has logically recovered the carnivore community that persisted in the Northern Rockies since the end of the Pleistocene. The species list of carnivores is the same as one that might have been written ten thousand or five thousand years ago. Having now restored the preexisting carnivore diversity, conservationists and managers face the problem of sustaining this system in a “healthy” manner. Ecological health can be examined within the varying time frames of ecological, community, and population dynamic processes. It can also be investigated over various spatial scales—landscape, ecosystem, community, or population. In this chapter we consider the question of conserving genetic biodiversity within the GYE’s carnivore species. Genetics cannot be isolated from other ecological processes, but maintaining genetic diversity is the necessary foundation for resolving conservation issues at higher levels of ecological organization. While concentrating on population genetic processes, we point out connections to these other levels.

In this chapter, we discuss the relevant genetic theory, current applications of molecular tools to carnivore genetic research, and ecological and behavioral data with genetic implications for GYE’s carnivores. We will explore genetic considerations for each species and place these in the context of management (e.g., Ralls and Ballou 1983). We will also touch on the implications of recent results for carnivore management in the GYE.

Genetics, Diversity, and Conservation of the Greater Yellowstone Ecosystem's Carnivores

The Carnivora occupy at least the third trophic level, and in general their body sizes are greater than those of their prey. In addition, they are warm-blooded and often must expend much energy to find sufficient prey over large home ranges or territories. Because of the reduced flow of energy to this trophic level, the thermodynamic constraints on its use, and the energetic requirements of relatively large-bodied animals, the maximum population sizes of carnivores tend to be small.

Table 11.1 shows very rough estimates of carnivore populations in the GYE, gathered from existing agency data or from the best guesses of field biologists. The GYE—a large, heterogeneous area of about 44,500 square kilometers—has not been systematically surveyed for most carnivores, and the accuracy of estimates for species varies greatly. Estimating total population size alone is difficult, and as we discuss below, social and reproductive behavior, degree of isolation, geographic features, population genetic history, and effects of human activities all work to reduce the genetic diversity within populations below that expected from a given census size.

For this discussion we will initially consider total numbers of adults (N) fewer than one thousand to constitute a small population, designated by an asterisk in table 11.1. The total population size (usually estimated as the number of adults) is not directly important in terms of genetics: an N of one thousand

Table 11.1

Body size and estimated number of Greater Yellowstone Ecosystem carnivores

| Species | Body size | Estimated N (adults) |
|---|-----------|------------------------|
| Grizzly bear (<i>Ursus arctos</i>) | large | < 400* |
| Black bear (<i>Ursus americanus</i>) | large | < 2,000 |
| Gray wolf (<i>Canis lupus</i>) | large | < 100* |
| Coyote (<i>Canis latrans</i>) | medium | < 3,000 |
| Red fox (<i>Vulpes vulpes</i>) | medium | < 2,000 |
| Mountain lion (<i>Felis concolor</i>) | large | < 500* |
| Bobcat (<i>Felis rufus</i>) | medium | < 500* |
| Lynx (<i>Felis lynx</i>) | medium | < 500* |
| Wolverine (<i>Gulo gulo</i>) | large | < 300* |
| Marten (<i>Martes americana</i>) | medium | < 10,000 |
| Fisher (<i>Martes pennanti</i>) | medium | < 200* |
| River otter (<i>Lutra canadensis</i>) | medium | < 500* |
| Badger (<i>Taxidea taxus</i>) | medium | < 1,000* |
| Striped skunk (<i>Mephitis mephitis</i>) | medium | < 2,000 |
| Mink (<i>Mustela vison</i>) | medium | < 3,000 |
| Ermine (<i>Mustela erminea</i>) | small | < 20,000 |
| Long-tailed weasel (<i>Mustela frenata</i>) | small | < 20,000 |
| Raccoon (<i>Procyon lotor</i>) | small | < 5,000 |

Note: * indicates a small population.

carnivores is well below Franklin's estimate of the genetic effective size needed to preserve adaptive potential (N_e of five hundred, or N of about 2,000, discussed below). The size of a population depends primarily on the amount of suitable habitat available (assuming human-caused mortality can be controlled). In the GYE, as a rule of thumb, the larger carnivores (bears, wolves, wolverines, and mountain lions) need much larger areas, and hence their populations are small. Smaller species such as otter, lynx, or fisher require less area, but their habitat (or prey) is restricted and thus their populations are also small.

In addition to small size, many of these populations in the GYE also show some effects of isolation, such as reduced heterozygosity. The movement of animals (and thus their genes) in and out of the ecosystem is restricted, and for many species movement between populations within the ecosystem is restricted. The central part of the GYE is a high-altitude, volcanic plateau with severe winters. The surrounding landscape is generally lower in elevation, supporting different habitat types and carrying the signature of human activity—a serious impediment to the movement of many carnivores.

Genetic and population genetic knowledge can enlighten and inform conservation decision making. We focus on the salient feature that, from the standpoint of many carnivore species, the GYE is an island ecosystem. The major management concern on islands is extinction, and in this chapter we explore the relation between genetics and extinction probabilities. Another genetic question is whether large enough island populations can be maintained to ensure long-term fitness and evolutionary potential (Soulé 1980). Such populations should be able to adjust to long-term environmental change. We feel that none of the GYE carnivore populations will ultimately be large enough to sustain sufficient levels of genetic diversity over millennia. Assuming that they will not remain that large, the next genetic question is whether the present population size has captured and can sustain sufficient genetic diversity to avoid short-term (decades or generations) loss of fitness through inbreeding and stochastic processes.

Genetic variation represents biodiversity within species (Cronin 1993). Alternate alleles represent options with which a species can respond to changes in the environment. Loss of variation limits the options and can increase risk of extinction. Fixation of alleles leaves a species with no genetic choice in subsequent generations unless mutation occurs. This may or may not be problematic, depending on whether or not the expression of a given allele is modified by other, perhaps more diverse alleles, and whether or not environmental changes have bearing on the trait in question. Thus loss of variation can make individuals more vulnerable to disease or climatic changes such as drought, increased cold, increased humidity, or increasing ultraviolet radiation. Effects on survival generally occur through inbreeding depression or susceptibility to disease.

EFFECTIVE POPULATION SIZE AND STOCHASTICITY

One of the consequences of small size and isolation is that genetic diversity can be reduced; genetic variation is related to population size (Frankham 1996). Deleterious genetic effects can hasten the extinction process through the short-term loss of fitness even in very small populations where the extinction threshold is within the range of demographic stochasticity. In populations that are large enough to exceed the range of demographic stochastic effects, genetic effects may act over time to reduce the population size enough that demographic effects become significant (Lacy 1997); this is the situation for most carnivores in the GYE because of the factors discussed in this section.

Effective population size, N_e , is a measure of the rate of loss of heterozygosity (inbreeding N_e). It also refers to the rate at which neutral alleles are lost from a population or the rates of fluctuation in allele frequencies (variance N_e). N_e represents the size of an ideal, randomly mating, panmictic population, which would have the same rate of allelic loss as the actual population being studied (e.g., Franklin 1980). Given that allele frequencies do not remain stable from generation to generation, such allele frequencies drift in value over generations and may end up fixed at either 0.0 (lost) or 1.0. Accompanying such drift is loss of heterozygosity (H) and loss of alleles. Neutral genetic variation, or heterozygosity, is lost over time in a finite population by random genetic drift and by behavior that produces inbreeding. Inbreeding, however, does not cause loss of alleles.

Because large mammals like carnivores tend to show many characteristics that may reduce the amount of variation that is passed on from generation to generation, N_e may be substantially lower than N , the actual population size. Among these characteristics are unequal numbers of breeding males and females, fluctuations in population size, non-Poisson distribution in progeny number (unequal reproductive success), and geographic genetic structure in the population (nonrandom mating patterns). When examining populations of wild animals, though, it becomes difficult to estimate parameters for these characteristics.

The standard formula for heterozygosity is written as equation 1 (Wright 1969):

$$H_t = H_0 [1 - 1/(2N_e)]^t \quad (1)$$

where H_0 = the amount of heterozygosity (H) at the beginning of a time period, H_t = the amount of heterozygosity (H) at the end of a time period, and t = the length of time in generations. The important point here is that N_e can be calculated from genetic data on heterozygosity. One can rearrange the terms in this equation to obtain equation 2:

$$N_e = [0.5]/[1 - (H_t/H_0)^{1/t}] \quad (2)$$

The problem with this approach is that it requires very accurate sampling of direct genetic data to determine the H levels, and H must be measured in at

least two sequential generations; for many GYE carnivores this can easily be a decade. With current genetic techniques, however, particularly microsatellite analysis (Paetkau et al. 1997), accurate estimates of H can be obtained.

We also have other methods to estimate the ratio of N_e to the census N . In effect we can estimate N_e from a "snapshot" of the genetic data using demographic data. Different formulas, however, describe different factors that can reduce N_e ; they are not alternatives but rather components that should be compounded to estimate the N_e resulting from multiple processes. Two important factors within a single generation are the ratio of males to females in the population and the variation in the sizes of families (Harris and Allendorf 1989, Hedrick and Gilpin 1996). One original formula (equation 3, Wright 1931) expressed N_e as a function of the number of successfully breeding females (N_f) and successfully breeding males (N_m):

$$N_e = 1/[1/(4N_m) + 1/(4N_f)] \text{ or } N_e = 4(N_m N_f)/(N_m + N_f) \quad (3)$$

For an ideal population, the sex ratio is one-to-one and the variance in family size is Poisson distributed. Deviations from either of these assumptions in natural populations lower N_e relative to N . Lande and Barrowclough (1987) give formulas with which to calculate these discrepancies. Harris and Allendorf (1989) used a simulation model to estimate N_e by tracing the loss of heterozygosity through time and then comparing results with estimates produced by applying published formulas.

Over multiple generations, N_e is more sensitive to the harmonic mean of the population sizes. Thus one low population size per one hundred years is very important in setting the average N_e over the century. For example, if the grizzly bear population is one thousand for ninety years and ten for ten years, the average genetic effective size for the century is ninety-one.

In wild populations of carnivores, N_e is always lower than N . Frankham (1996) found that estimates of N_e/N varied according to fluctuation in population size, variance in family size, form of N used (adults, breeders, or total size), taxonomic group, and unequal sex ratio. Wilcox (1986) estimated the ratio of (N_e/N) to be 0.25 in mammals as a rule of thumb. Harris and Allendorf (1989) estimated a ratio of 0.24 to 0.32 for grizzly bears. Using only Wright's original equation and estimating the number of breeding males from paternity results of microsatellite analysis, two of the authors (Craighead 1994, Craighead and Vyse 1996) estimated an N_e/N ratio of 0.41 in an Arctic grizzly population.

Recent results from microsatellite analysis (Paetkau et al. 1997) demonstrate that the N_e to N ratio for grizzly bears may be only 0.037–0.12 (depending on the mutation rate). Whatever the actual value of N_e , it is clear that carnivores have effective population sizes that are much smaller than the actual numbers of animals censused.

Genetic stochasticity. Random (stochastic) events, or sampling effects, play a large role in the dynamics of small populations. As population size fluctuates near the extinction threshold, such factors as demographic stochasticity, genetic stochasticity, environmental stochasticity, and catastrophic events pose immediate risks (Shaffer 1978). Demographic stochasticity can rapidly reduce population size when N is below about twenty-five (Gilpin 1992). These four factors can be considered as extrinsic (environmental stochasticity and catastrophe) or intrinsic (demographic stochasticity and genetic deterioration) to a species (Hedrick 1996). Caughley (1994) coined the phrase "small population paradigm" for the approach focusing on effects of these four factors. He contrasted this to the "declining population paradigm," which focuses on deterministic factors such as habitat destruction, overkill, and fragmentation (Diamond 1989). Many researchers feel that deterministic factors such as human-caused mortality are the overriding cause of concern for many species such as grizzly bears (e.g., Primm 1996, Mattson et al. 1996, Peek et al. 1987). However, all these factors are interrelated in causing the decline of populations and eventual extinction, and genetic factors can be critical even in very small populations (Mills and Smouse 1994). The relative importance of each factor will vary in each situation.

Many of the larger carnivore populations may currently be at low enough levels that genetic effects could nudge them into the realm of demographic stochasticity in just a few generations, greatly increasing their risk of extinction. For medium-sized carnivores with larger population sizes, genetic factors can have long-term effects that act to reduce population sizes gradually, especially if movement between populations is restricted. For all carnivore species, a prudent approach is to conserve as much genetic variation as possible in order to avoid augmenting negative demographic effects, to allow an adaptive response to modified environmental conditions, and to stockpile against future evolutionary change (Soulé 1980).

GENETIC DIVERSITY IN TIME AND SPACE

The level of genetic diversity is controlled by five population genetic processes—mutation, migration, selection, drift, and inbreeding (e.g., Hedrick 1985)—which in turn are regulated by the size of the population, its biotic and abiotic environment, and its spatial structure. Thus the unique physiography of the GYE and the unique physiology of its inhabitants, communities, and systems impose limits and provide opportunities for genetic interplay. We are only beginning to understand how genetics are shaped by these processes in a spatially explicit setting, but the GYE provides a natural laboratory where some of these questions may be answered. Carnivore population genetics are affected

by the basic processes outlined below, and carnivores themselves influence the genetics of other species.

Mutation. The processes of mutation and changes in allele frequency determine the amount of genetic variability within a closed population (that is, one with no immigration or emigration). Mutation is the inherent process whereby organisms change from one hereditary state to another (Suzuki et al. 1989). It can be in the form of a gene (or point) mutation, where one allelic form mutates to another, or a chromosome mutation, which refers to changes in chromosome structure or number involving segments of chromosomes, whole chromosomes, or even sets of chromosomes. Only mutations in reproductive (germline) cells can be transmitted to progeny. Different portions of the genome exhibit different mutation rates. Mitochondrial DNA (mtDNA) rates are estimated at 10 percent substitution of nucleotides per million years in mammals (Irwin et al. 1991). Microsatellite mutation rates are probably between 1×10^{-3} and 2×10^{-4} per generation (Amos et al. 1996, Paetkau et al. 1997). Most mutations are probably selectively neutral and do not affect the survival of the organism. Mutations are rare events and thus are less likely to occur in small populations.

Migration. Most carnivore populations are not closed systems, however, because animals disperse from their natal areas. Over time, unique alleles appear through mutation and become locally established in a population. If individuals carrying those alleles disperse into another population and breed successfully, those alleles can be introduced. The movement of alleles between populations (or subpopulations) is termed gene flow. At any point in time, different populations may exhibit different frequencies of each allele (except where fixed). The more frequent the interchange of individuals between populations, the greater the amount of gene flow and the closer the allele frequencies will be to each other.

Natural selection. Allele frequencies are also modified by selection. If environmental factors change enough so that one phenotype (and the alleles responsible) is selected for, or against, the frequencies of those alleles will increase or decrease. Over time, localized genetic differences arise as a population becomes more closely adapted to its immediate environment. There are thus two components that produce differences in allele frequencies between populations: random differences resulting from drift, and selected differences resulting from enhanced survival and reproduction conferred upon certain alleles.

If a population becomes totally isolated, or closed, it will diverge genetically from other populations over time because of the effects of drift and selection. At some point this will result in a locally adapted population that is sufficiently

divergent (reproductively isolated) from its ancestral population that it can be considered a separate species (e.g., Mayr 1991).

Genetic drift and inbreeding. Changes in allele frequencies in small populations result primarily from random processes. Deviations from the expectations of randomness in population genetics data imply that some other process such as selection, nonrandom mating, or geographic separation may be at work. Alleles that are rare in a population (such as those that recently appeared by mutation) may not appear in the next generation because of random sorting, or genetic drift. Other alleles may increase in frequency. As the frequency of an allele increases, so does the probability of its persistence in the gene pool. Over the progression of generations, allele frequencies can drift as a result of sampling effects (drift) with the ultimate fixation of one allelic form at each locus. The effects of drift are increased in small populations.

LOSS OF GENETIC VARIABILITY

Inbreeding depression. In small populations, mate choice is limited and individuals become more closely related over time. Heterozygosity can be lost by inbreeding (the mating of closely related individuals, which is measured by Sewall Wright's F_{is}) or by random sorting of alleles in a small population (which is measured by divergence among populations, Wright's F_{st}). Loss of heterozygosity increases the chance that harmful recessive alleles will be expressed (Ralls et al. 1986). This expression of harmful alleles in the phenotype acts in a variety of ways to depress fitness by lowering fecundity and reducing survival rates. A concise discussion of the importance of genetic variation can be found in Lacy 1997.

The term *inbreeding depression* refers to a decrease in fitness, regardless of how heterozygosity is lost. The rate of inbreeding is generally measured by the reduction in heterozygosity (H) per generation. Heterozygosity has shown no correlation with fitness in several studies (Hedrick 1996), but lowering of H has been demonstrated to be positively correlated with reduced fitness in many other populations (Allendorf and Leary 1986, Ralls and Ballou 1983). The deleterious effects of inbreeding depression can be difficult to detect, particularly in small populations of mammals or birds. Inbreeding depression is generally expressed as reduced fertility or low juvenile survival (Ralls et al. 1979). Correlations between low heterozygosity and reduced juvenile survival in mammals have been demonstrated in inbred ungulates (Ballou and Ralls 1982), as well as in other species, including carnivores. Inbreeding has also been used to explain increased vulnerability of animals to disease (e.g., O'Brien and Evermann 1988).

Domestic animal breeding experience indicates that a 1 percent rate of inbreeding per generation is the maximum allowable to avoid the increased ex-

pression of deleterious alleles that have been exposed in homozygotes (Franklin 1980). The extent to which these generalizations are applicable to carnivores is not clear, but carnivores may tend to be less outbred than other mammals. Paetkau et al. (in press) found a reduction of heterozygosity of 15–20 percent over the past one hundred years in grizzly bears in the CYE, assuming that this population was once contiguous with and similar in variability to grizzlies in the Flathead River. This corresponds to a 1–4 percent rate of inbreeding.

However, reduced heterozygosity may or may not be immediately harmful in a given population. Thus elephant seals were able to pass through a population bottleneck of about one hundred individuals with a significant loss of allelic diversity and rebound to a current population of about 150,000. Hawaiian monk seals, on the other hand, after a similar bottleneck, continue to decline and now number about 1,300 (Kretzmann et al. 1997).

Thus species may differ in their sensitivity to inbreeding, depending on which alleles are lost. Inbreeding depression may not be manifested until a change in the environment provides an opportunity for other genetic options that have been lost through inbreeding. This may occur even in apparently highly successful species. Reduced genetic diversity therefore constitutes an increased risk of extinction to a population or a species: alleles that are lost in small populations might be important to survival now or at some time in the future under different conditions. No species of mammal has been shown to be unaffected by inbreeding, and genetic threats to viability will be expressed through their effects on and interactions with demographic and ecological processes (Lacy 1997).

Inbreeding in normally outbreeding species generally has deleterious effects. There is a possibility that harmful recessives can be purged from the population after a bottleneck, leaving the genome with less genetic load (accumulated deleterious genes) than before, but there is little evidence as yet (Lacy 1997). Though strongly deleterious recessive alleles may be removed in this fashion, overdominant or weakly deleterious recessives will remain (Ballou 1997, Hedrick 1994).

Genetic variation and spatial constraints. Conservation genetic research focuses on understanding the relation between genetics and the persistence of local populations, and this knowledge is used to sustain the fitness of small populations (Ralls and Ballou 1986). Lacy (1997) reviews evidence that lower genetic variation depresses individual fitness and mean fitness of populations. Frankham (1996) examines the relation between population size and genetic variation—the larger the population, the more variation. He also concludes that genetic variation within a species is related to “island” size or the amount of habitat a population can occupy.

Genetic variability is generally measured as the degree of heterozygosity. Although our models often concern single genetic loci, it is the genome-wide heterozygosity that is most useful for conservation analysis and conservation decision making. Heterozygosity is a relative concept. For small populations, we are interested in the level of heterozygosity relative to large, secure, mainland populations (if such exist) and in the internal spatial structure of heterozygosity within the conservation reserve.

Populations can originate with very low variability as a result of the founder effect. Two or more individuals may colonize unoccupied habitat, as when a species expands its range or when habitat has been vacated by a local extinction event. The total genetic diversity of the new population is low relative to other, larger populations. Without additional migration, the genetic diversity will remain low and will be further reduced by inbreeding. Species that were greatly reduced in number in the GYE, such as mountain lions and wolverines, have undergone genetic "bottlenecks" that probably lowered genetic diversity, but not as severely as a founding event.

Genetic variability is also influenced by population genetic structure, or subdivision: localized genetic differences within a population of interbreeding individuals. Differences in genotypes between populations, or between subgroups of populations, may reflect differential fitness values or local adaptation. Variation expressed as genetic structure can be viewed as a component of genetic diversity that has survival value for the population as a whole and is important for the conservation of the population or species as a whole.

Such differences can be caused by such nonrandom factors as assortative mating or from historical factors and drift. Gene flow, or the movement of alleles between component populations, acts to decrease genetic subdivision. The primary mechanism of gene flow in carnivores is dispersal of subadult animals. A subdivided population can theoretically maintain a greater amount of genetic variation than a single, large, panmictic population (Hedrick 1996, Hedrick and Gilpin 1996), as long as the subpopulations are stable.

GENETICS AND CARNIVORE CONSERVATION

To conserve carnivores we need to understand the genetic "health" of the populations in the GYE primarily through the measurement of heterozygosity and allele frequencies, and we need to understand the "structure" of this variation within and between population components. Overall, we need to examine the GYE as a conservation reserve, a refuge from extinction. In this section we shall discuss the genetic aspects relevant to species conservation—how genetic variation is measured, how much is enough, and how can we maintain that much.

Genetic tools and genetic markers. There are various molecules, markers, and methods that are applicable to the study of carnivore genetics. A genetic marker is an allele that can be marked or labeled and used as an experimental probe to keep track of an individual, tissue, cell, chromosome, or gene through the hereditary process. A genetic tool is a technique for manipulating DNA, DNA fragments, alleles, or proteins in order to identify and trace genetic markers through generations or populations.

There are three classes of molecules commonly studied: proteins, mitochondrial DNA, and nuclear DNA. Variation in these molecules at the level of species, populations, or individuals can be addressed using different analytical techniques. Because each focuses on a particular portion of the genome with varying degrees of resolution, different tools may produce different results when applied to the same genetic sample (for example, mtDNA reveals little about patterns of relatedness within family groups). This is important to keep in mind when interpreting results: methods appropriate to the spatial scale must be used.

The first tool is protein electrophoresis. Techniques of protein analysis focus on identifying and enumerating proteins, or allozymes, which are products of protein synthesis and indirectly reflect the underlying allelic variation. Protein electrophoresis is useful for comparing allele frequencies between populations or estimating genetic distances between species. Additional information relative to carnivore populations can be found in Goldman et al. (1989), Cronin (1993), and Hedrick (1996).

The second tool is DNA analysis. Techniques of DNA analysis focus on identifying and enumerating alleles (either directly or indirectly via "fingerprints"). The occurrence of a variety of alleles in a population (each individual has only two out of all alleles available) is important to produce a variety of genotypes and phenotypes, some of which may allow a population to survive and evolve under changing conditions. Factors that tend to reduce the amount of genetic variability in a population reduce its phenotypic options and thus reduce its chances for long-term survival. Analysis of the actual genetic material, DNA, allows quantification of the allele differentiation. These differences can be addressed by looking at multilocus groups or at single loci. Discussion of relevant DNA applications can be found in Cronin (1993), Talbot and Shields (1996), Paetkau and Strobeck (1994), Paetkau et al. (1995), and Kohn et al. (1997).

Rules of thumb for genetic management. An N of twenty-five is often used as a threshold for the effects of demographic stochasticity (Gilpin 1992). Both Franklin (1980) and Soulé (1980) estimated a minimum of fifty effective breeding individuals to maintain short-term fitness, and five hundred to maintain standing genetic variation. This "50\500 rule" has often been adopted as a

guideline for conservation (Wilcox 1986), although there was little empirical basis for it. Subsequent analysis suggested a rule of thumb of five thousand to maintain standing genetic variation (Lande 1995).

A closed population will lose alleles through random events, or drift, while an open population may recover lost alleles through migration. One successful migrant individual per generation has been estimated as the minimum necessary to maintain an allele in a distant population (Wright 1969). Mills and Allendorf (1997) suggest that one migrant per generation may be an acceptable minimum, and ten migrants per generation is probably not too much to swamp localized differences in allele frequencies, but there are many mitigating factors in each population that make rules of thumb unreliable.

All of these rules or rough genetic guidelines were offered by their authors with cautionary caveats. They point out that every population has different effective population size, levels of variation, connectedness to other populations, and genetic history. In addition to deciding what population size is adequate for a desired genetic outcome, managers are faced with many other constraints. Often political, economic, or traditional considerations will interfere with optimal biological solutions. However, we are reaching a level of technological expertise that should make it possible to define the genetic health of a given population as a baseline for protecting genetic diversity. Rules of thumb are valuable tools for a first approximation, particularly when time is short and habitat is disappearing, but the techniques and approaches discussed below point the way toward measuring genetic diversity and prescribing more-precise spatially and numerically explicit solutions.

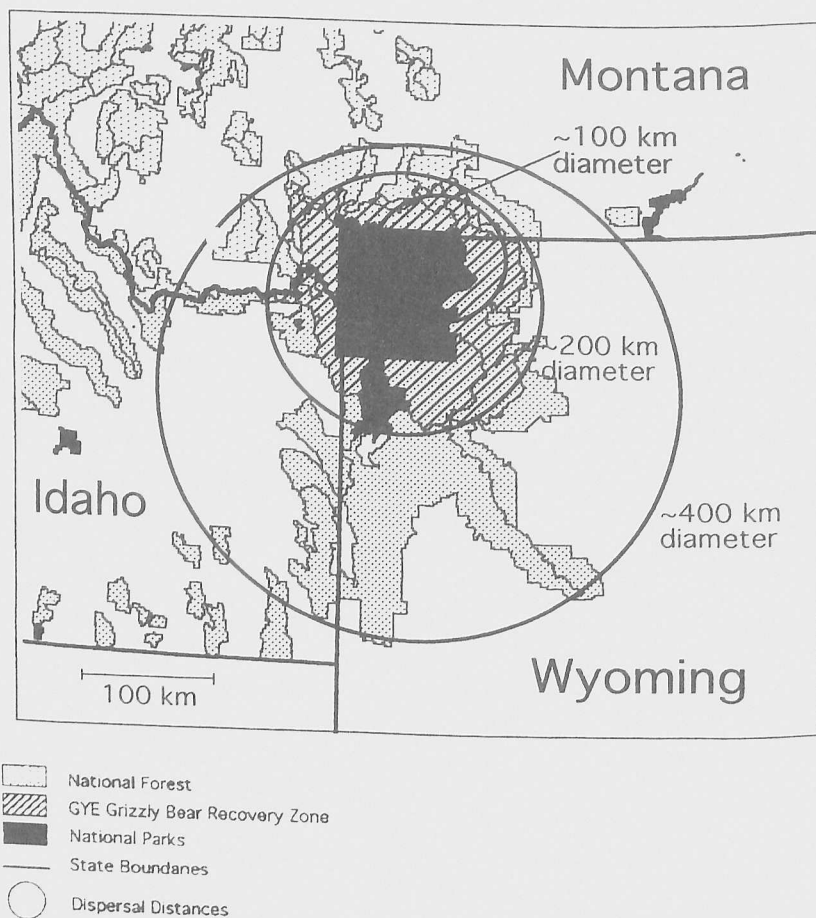
Genetics and reserve design. Shaffer (1987) introduced a systems approach to the study of extinction, distinguishing between deterministic and stochastic factors. Gilpin and Soulé (1986) further refined these ideas. The concerns for survival of small populations are: (1) deterministic extinction, which occurs when something essential (such as space, shelter, or food) is removed or when something irretrievably negative is introduced, (2) environmental stochasticity, or random changes such as drought, global warming, or severe winters, (3) demographic stochasticity, or the chance variation in individual birth and death events, which has very large effects once a population becomes very small, (4) genetic deterioration, which can reduce fitness through increased genetic drift, inbreeding, and the subsequent loss of heterozygosity and genetic variance, and (5) catastrophes, or rare but widespread events that can extinguish a population or species, such as a huge meteorite, an epic flood, or the eruption of a large volcano. (The latter event formed the Yellowstone plateau and may have caused the extinction of several populations and perhaps even species.)

To reiterate, a conservation reserve can be considered a refuge from extinction. An adequate reserve will buffer a species from these five concerns for a certain length of time. A key concept in reserve design is the equilibrium theory of island biogeography (MacArthur and Wilson 1967, Harris 1984). This theory quantifies the number of species on an island as a function of the immigration rate, the extinction rate, the area of the island, and its distance from the mainland source of immigrants. The number of species on the island reaches an equilibrium, and although the number of species stays about the same, the composition of the fauna will change as species come and go. This theory is germane to our discussion because the GYE can be seen, from the viewpoint of many carnivore species, as an island of habitat.

To maintain carnivore populations over long time periods (tens or hundreds of generations), nature reserves need to be large enough to support an effective population size in which there is no significant loss of genetic diversity. Single large reserves, or groups of connected reserves, should ideally be large enough to contain subdivided populations (genetic structure) and therefore to conserve more genetic diversity within a species (Hedrick 1996, Hedrick and Gilpin 1996). A reserve the size of Greater Yellowstone may not be large enough to encompass and conserve genetic structure for large carnivores such as grizzly bears (Craighead et al. 1995), wolverines, or wolves but may capture this level of genetic diversity for other carnivores.

Frankel (1970) was probably the first to recommend genetic considerations in designing nature reserves. Schoenwald-Cox (1983) elaborated on the idea. Estimates of minimum population sizes and minimum area requirements have varied greatly, but as genetic techniques and understanding improve, these estimates are beginning to converge.

The GYE (figure 11.1) contains about 44,500 square kilometers of undisturbed roadless area, 17,800 square kilometers of which have no legal protection (Harting and Glick 1994). The Greater Yellowstone Grizzly Bear Recovery Zone covers an area of 24,605 square kilometers (USFWS 1993). Frankel and Soulé (1981) estimated that mountain lions would need about 13,000 square kilometers of habitat to survive, and wolves would need 39,000–78,000 square kilometers. Metzgar and Bader (1992) estimated that 129,500 square kilometers of habitat would be needed to maintain an N_e of five hundred grizzly bears. Paquet (unpublished, reported in Noss et al. 1996) estimated that wolves may require four times as much habitat as grizzly bears—518,000 to 1,295,000 square kilometers. Salwasser et al. (1987) estimated that the GYE may be the only place that could support 2,500 grizzly bears (an N_e of 625, according to Wilcox 1986). At the upper extreme, large mammals, with effective population sizes in the hundreds, may require 500,000 square kilometers of habitat for a 95 percent



11.1. The Greater Yellowstone Ecosystem, showing national park and forest lands, the grizzly bear recovery zone, and bear dispersal distances.

probability of persistence for one thousand years (Belovsky 1987, Shaffer 1987).

These estimates are, of course, inexact, but the trend is clear: very large reserves are needed for long-term persistence. Reserves of such size may be possible only in the Arctic. In Greater Yellowstone we must focus on lower certainty and explore other options for providing adequate habitat for carnivores. Recent theories of reserve design have focused on the *sloss* question—that is, should there be “single-large-or-several-small” reserves (Diamond 1976, Gilpin and Diamond 1988)—and on the provision of travel corridors between reserves (Noss et al. 1996, Beier and Noss 1998).

As far as large carnivores are concerned, the GYE is one large reserve. The core of this reserve is protected by law, but additional large, relatively roadless areas surround the core. Dispersal distances and the likelihood of gene flow between distant populations within and without the GYE are discussed below. At the very least, it seems crucial to maintain existing undisturbed habitat by appropriate conservation mechanisms (legal protection, conservation easements, land trades, and so on) and to maintain functional habitat connections (Noss et al. 1996) with other large reserve areas. Weaver et al. (1996) suggest that cougars and wolves may be maintained more successfully in a network of refugia spaced within dispersal distances (on a regional scale), while grizzly bears and wolverine may fare better in larger and more contiguous reserves.

Population Genetics of Greater Yellowstone Carnivores

From a management perspective, maintaining genetic diversity in carnivores requires populations large enough to contain historic levels of heterozygosity and to maintain historic levels of gene flow between subpopulations. In many cases, most notably the larger carnivores, these historic levels have already been lost, and we have no genetic baseline against which to compare current populations. We can only look at similar-sized populations in somewhat similar habitat to estimate the historic levels for the GYE. For the medium and smaller-sized carnivores, population size and genetic diversity have probably not been reduced critically from historic levels.

Population genetics is the study of gene (allele) behavior in populations. Research at this level is expanding rapidly with the advent of new tools. Below, for each family of Carnivora, we first discuss recent genetic research and its relevant findings. Since alleles are carried by individuals, dispersal and breeding behavior are important variables in understanding gene flow and genetic diversity. Next, for each family, we review behavioral and ecological studies that have bearing on the species and the environment of the GYE.

Dispersal patterns of subadults as they reach sexual maturity are an exceedingly important factor determining gene flow, population genetic structure, and ultimately genetic diversity. In mammals, the general pattern of dispersal seems to be that males are more mobile, while females remain nearer to their natal areas (Greenwood 1980). One reason may be that group-living mammals are primarily polygynous (Eisenberg 1981); subordinate males are excluded from breeding and forced to move to other groups to increase their reproductive potential. In monogamous species, both females and males are excluded from breeding by a dominant pair, and both sexes may need to disperse to reproduce (Rood 1987).

Table 11.2

Home range/territory size and dispersal distances of large and medium-sized carnivores

| Species | Home range/territory size (km ²) | | Male dispersal distances (km) | |
|---------------------|--|-----------|-------------------------------|---------|
| | Mean | Range | Mean | Maximum |
| Gray wolf | 900 | 210-1,700 | 85 | 917 |
| Coyote | 5.6 | — | 48 | 81 |
| Red fox | 5.3 | 0.19-0.72 | — | — |
| Grizzly bear, male | 1,000 | 233-1,970 | 70 | 300 |
| female | 450 | 72-874 | — | — |
| Black bear, male | 120 | 53-225 | — | — |
| female | 20 | 14-137 | — | — |
| Mountain lion, male | 889 | 78-1,000 | — | 480 |
| female | 117 | 45-373 | — | — |
| Lynx, male | 200 | 145-250 | 300 | 1,100 |
| female | 70 | 51-122 | — | — |
| Bobcat, male | 122 | 21-200 | 109 | — |
| female | 43 | 18-59 | — | — |
| Wolverine, male | 422 | 200-1,500 | 50 | 378 |
| female | 388 | 105-400 | — | — |
| Fisher, male | 40 | — | 50 | 100 |
| female | 15 | — | — | — |
| Marten, male | 5 | — | 27 | — |
| female | 3 | — | — | — |
| Badger, male | 1.4 | — | — | — |
| female | 1.2 | — | — | — |

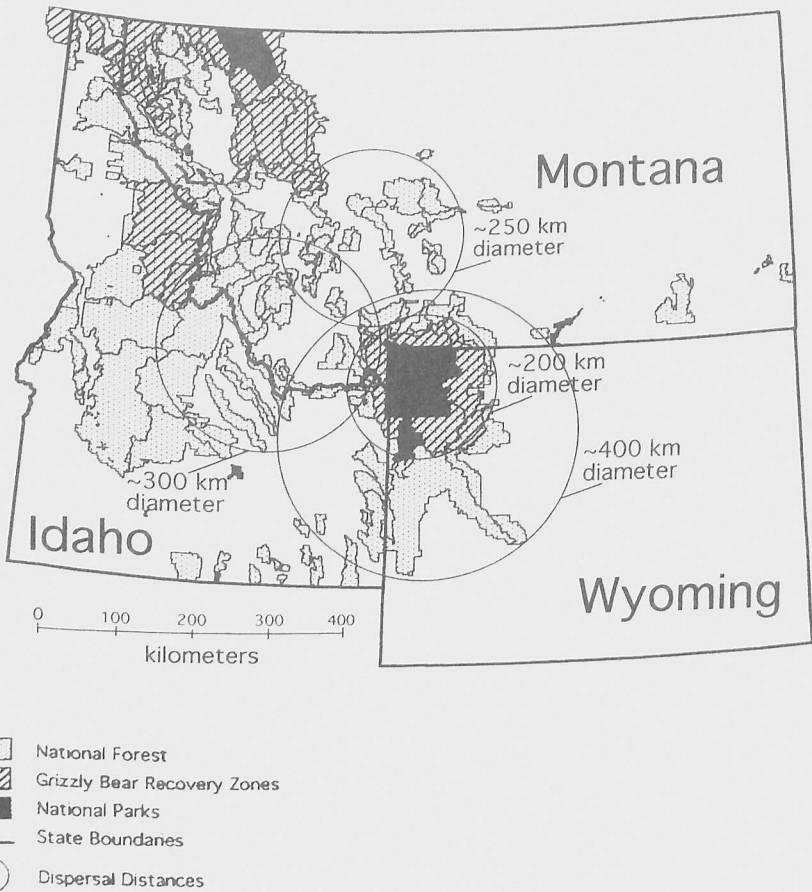
Note: Data from across North America.

It is generally hypothesized that dispersing animals will occupy the first unoccupied habitat they encounter. However, there are instances where dispersers are tolerated within adult home ranges, and other instances where dispersers travel long distances even though suitable habitat appeared to be nearby.

Dispersal distances are summarized in table 11.2, with details and citations discussed below. These are estimates, extrapolated in some cases from the literature, to convey a rough sense of the spatial requirements of these species and the distances necessary for genetic subdivision and restriction of gene flow.

There are few data on genetic structure of carnivore populations in the GYE (or elsewhere, for that matter). Some inferences can be made by examining typical distances of home ranges and dispersal movements. If known centers of distribution are separated by distances greater than known dispersals or by barriers to movement, it is possible that they are isolated to some degree and have diverged genetically, creating a subdivided population or metapopulation.

At a regional scale (figure 11.2), broad forested dispersal routes exist between the GYE and the Northern Continental Divide Ecosystem (NCDE) and the Salmon-Selway Ecosystem (SSE). These areas are currently occupied by cougars



11.2. Grizzly bear recovery zones in Montana, Idaho, and Wyoming in relation to national park and forest lands in the Greater Yellowstone Ecosystem, the Northern Continental Divide Ecosystem, and the Salmon-Selway Ecosystem.

and have historically been occupied by grizzlies. Merriam (1922) reported grizzlies occupying the Tobacco Root, Gravelly, Crazy, Little Belt, Snowy, and Sapphire mountain ranges. Aune (personal communication) knew of grizzlies in the Big Belt Mountains in the early 1960s. Between 1976 and 1984 grizzlies were observed (or killed) in the Gravelly, Tobacco Root, Highland, Champion-Thunderbolt, and McDonald-Rogers mountain ranges (Picton 1986). Picton estimated that 3,600 square kilometers of habitat encompassing the Tobacco Roots, Snowcrests, and Gravellys could support about thirty-nine bears, while habitat farther north along the Continental Divide (3,250 square kilometers)

Table 11.3

Summary of carnivore genetic status in the Greater Yellowstone Ecosystem

| Species | Genetic health | Genetic structure | Isolation |
|---------------|------------------------|-------------------|-------------------|
| Wolves | <i>Normal - high H</i> | None | Moderate |
| Coyotes | <i>Normal H</i> | Little | None |
| Red foxes | <i>Normal H</i> | Moderate | Moderate |
| Grizzly bear | <i>Low H</i> | <i>None</i> | <i>High</i> |
| Black bear | <i>Normal H</i> | Little | None - little |
| Mountain lion | <i>Normal H</i> | None - little | None - little |
| Bobcat | <i>Normal H</i> | Little | None |
| Lynx | <i>Low - normal H</i> | Little | Moderate |
| Wolverine | <i>Normal H</i> | Little - none | Little - moderate |
| Fisher | <i>Normal H</i> | Little | Moderate |
| Marten | <i>Normal H</i> | Moderate | Little |
| Otter | <i>Normal H</i> | Moderate | Little |
| Badger | <i>Normal H</i> | Moderate | Moderate |
| Weasels | <i>Normal H</i> | Moderate | Moderate |
| Skunks | <i>Normal H</i> | Little | Little |

Note: Items italicized are based upon some relevant genetic data.

could support about thirty-three. If managed with that goal in mind, these areas could support small populations of grizzly bears and wolves, as they already support other carnivores. Gene flow and population rescue could occur in the GYE for bears, wolves, cougars, and other species as long as dispersing animals could negotiate the filters and barriers (primarily human-caused) between islands of habitat.

Below we discuss the carnivore families in the GYE in light of current knowledge. Those species with normal to high heterozygosity (*H*), some degree of genetic structure within or between populations, and little to no isolation from other populations stand the best chance for long-term persistence. Table 11.3 summarizes our current state of knowledge (often no more than best guesses) of the major species.

CANIDAE: FOXES, COYOTES, AND WOLVES

The Canidae of the GYE consist of species with wide distribution. Although research here has focused mainly on coyotes and wolves, and mostly within the past decade, these species have been studied elsewhere and much of this research is directly applicable.

Current genetic research. Forbes and Boyd (1996, 1997) discussed microsatellite variation in naturally colonizing wolves in Glacier National Park, other Rocky Mountain populations, and reintroduced populations. They found high levels of genetic variation in multiple, unrelated founding wolves from Canada. They concluded that wolves in the United States and Canada in the

Rocky Mountains should be viewed as a single population and that maintaining gene flow throughout the region is necessary to retain this genetic variation. Wolf dispersal over long distances is likely if legal protection and public tolerance is adequate. Differentiation and hybridization of wolf and coyote populations has also been studied using microsatellite loci (Roy et al. 1994). Introgression of coyote mtDNA into gray wolf populations was demonstrated in Minnesota wolves (Lehman et al. 1991), demonstrating ancestral breeding between wolves and female coyotes. Twenty-six populations of gray wolves in North America were examined for mtDNA variability: eighteen genotypes were found, seven of which were derived from hybridization with coyotes (Wayne et al. 1992).

Little genetic research has been conducted with coyote populations. Results include the introgression studies discussed above (Lehman et al. 1991) and a mtDNA survey across North America in which coyotes showed no significant genetic differentiation, even between distant populations, and had six times as many genotypes as wolves (Lehman and Wayne 1991). This similarity is attributed to high rates of gene flow because of a rapid recent increase in coyote numbers and the expansion of their range (Wayne et al. 1992). Unhunted coyote populations in the GYE have established social behavior similar to wolves (Crabtree personal communication). Introgression between these species after wolf reintroduction is a distinct possibility.

Foxes have received little attention in the GYE. Red foxes from the Absaroka-Beartooth Plateau exhibit striking morphological differences from other areas (Crabtree personal communication), which may indicate genetic differences and population structure.

Patterns of dispersal. Coyotes and wolves tend to form social packs with a dominant breeding pair. Red foxes typically breed monogamously but also form polygynous groups of one male and two to five females (MacDonald 1981). Both sexes of juvenile wolves disperse and attempt to join other packs (Mech 1987); this is also the case in coyotes. Dispersal group size and timing of both wolves and coyotes appears to be influenced by local prey species and population density (Bekoff and Wells 1980). Where coyote population density is high, group size is larger (Andelt 1982). Wolves commonly travel fifty kilometers or more per day (Paquet personal communication), and males have been recorded traveling up to 917 kilometers (Fritts 1983). A young female dispersed 840 kilometers (Boyd et al. 1996). Wolf dispersal distance averaged over many studies is about eighty-five kilometers, with male dispersal only about eight kilometers greater than female (Weaver et al. 1996). High-volume roads like the Trans-Canada Highway near Banff are a barrier to wolves, but low-volume roads are

crossed easily. Some wolves will use underpasses, but others will not (Paquet personal communication). Coyotes disperse in two modes in the GYE (Crabtree personal communication); either about fifty kilometers completely away from the natal area or into neighboring territories of other packs. The longest recorded dispersal distance for a coyote was 544 km (Carbyn and Paquet 1986).

Population sizes, home ranges, and inferences of genetic structure. Wolves were extirpated from Yellowstone Park (and the GYE) beginning in the 1870s by hide hunters poisoning elk carcasses, and a concerted effort to eliminate them was carried on from 1914 to 1926. The last two wolves killed by federal agents in the park were trapped in 1926, but a handful seem to have persisted into the 1930s, and one was killed in the GYE in 1943 (Varley personal communication). Thirty-one wolves were reintroduced into the GYE in 1995 and 1996 by the U.S. Fish and Wildlife Service and National Park Service under mandates of the Endangered Species Act. There were fifty-two known wolves by the winter of 1997 (Varley personal communication) and probably close to one hundred by late spring (Maughan personal communication). Wolves were captured in Alberta from presumably unrelated packs from different areas with the goal of introducing a genetically diverse founder population. It will be several generations before the population stabilizes, but distribution may eventually focus on two or three geographic areas, such as northern Yellowstone and geyser basins, Jackson Hole, and perhaps the Wind River Range foothills. A critical factor will be the availability of winter prey. Territory sizes of wolf packs range from 780 to 1,040 square kilometers in northwestern Montana. Lone wolves may range over 2,600 square kilometers (USFWS 1994). Wolves disperse long distances and gene flow occurs on a regional scale (Forbes and Boyd 1996, 1997). In light of this mobility, genetic subdivision probably occurs between the large core reserves but not within any of them.

Coyote populations are stable throughout Greater Yellowstone. High levels of gene flow discussed above should mitigate any genetic structure among areas within the ecosystem, but the lack of wintering habitat in the central Yellowstone Plateau may act as a partial barrier to dispersal between the northern and southern parts of the ecosystem. Coyote densities are probably highest in the Northern Range of Yellowstone Park where they average about 0.5 to 1.0 coyote per square mile. Territory size averages about 5.6 square kilometers (3.0 square miles, Crabtree personal communication). Throughout the entire ecosystem there are probably fewer than three thousand coyotes.

Red foxes appear to be stable in moderate numbers throughout the ecosystem. There are about two thousand in the entire GYE (Crabtree personal communication). Home-range sizes have been reported elsewhere as small as 0.19

to 0.72 square kilometers (MacDonald 1981) or as large as 5.3 square kilometers (Von Schantz 1981).

URSIDAE: BLACK AND GRIZZLY BEARS

Of the GYE's two bear species, the grizzly has been the subject of much more research, both ecological and genetic. Black bears, on the other hand, have been more or less taken for granted by the scientific community and even rough population estimates are uncertain.

Current genetic research. Allendorf and Knudsen have examined isozyme variation in grizzly bears and polar bears. Varying levels of polymorphism were found in different populations, with the least variation in grizzly bears from Kodiak Island (Knudsen personal communication). Cronin et al. (1991) found five mtDNA haplotypes in brown bears from sample locations from Alaska and Montana. Further mtDNA analysis by Waits et al. (1997) resolved four clades in North America that were probably formed before migration of the species from Asia. Three evolutionarily significant units are suggested; the GYE population is grouped with southern Alberta and British Columbia, Idaho, Montana, and Wyoming (Waits et al. 1997).

Simulations indicate that existing grizzly bear populations in the lower forty-eight states are not large enough to avoid detrimental loss of genetic variation in the short term (Harris 1986, Harris and Allendorf 1989). An initial small sample of sixteen grizzly bears from the northern Rockies was not found to differ significantly from Alaskan populations in heterozygosity, but five unique microsatellite alleles were found (Craighead 1994). However, analysis of a larger sample of 667 grizzlies, seventy-two of which were from Yellowstone, demonstrated a significantly lower H (55 percent) for Yellowstone grizzlies, compared with a high of 76 percent in the Kluane sample ($N = 50$) and a low of 26 percent in the Kodiak sample ($N = 34$). The main factor affecting levels of genetic diversity appears to be connectedness to larger populations (Paetkau et al. 1997). Estimates of N_e can be obtained from H within the limits of the accuracy with which mutation rates are known (assuming equilibrium for mutation, genetic drift, and migration). Thus estimates of N_e for the Yellowstone population are thirteen to sixty-five effective grizzly bears (Paetkau et al. 1997).

Zimmerman (1989) examined Restriction-Fragment Length Polymorphism variation in mtDNA among fifty-five black bears. Minor differences were found between three subspecies. Cronin et al. (1991) found six mtDNA haplotypes in black bears. Black bears ($N = 40$) examined were from Alaska, New Hampshire, Oregon, and Montana. Two genetically distinct groups of black bear haplotypes were found, and some types were found in only one location. Paetkau and

Strobeck (1994) examined genetic variation in black bears using four microsatellite loci. Black bears isolated on the island of Newfoundland were found to have relatively reduced levels of variation, analogous to brown bears on Kodiak.

Patterns of dispersal. Bear dispersal patterns follow the general mammalian pattern: females are more philopatric and often share a portion of their natal home range with the mother (Reynolds and Hechtel 1984). Males disperse farther, occasionally traveling hundreds of kilometers (Craighead 1994). In the GYE four dispersing males moved an average of seventy kilometers from their natal home range (Blanchard and Knight 1991). This pattern persists despite the fact that both brown and black bears exhibit characteristics of polygyny and polyandry. Male grizzly bears have been known to breed successfully with more than one female during a single season, and females have bred successfully with more than one male, producing litters with multiple paternity (Craighead et al. 1995). Factors other than breeding exclusion, therefore, also appear to be involved in dispersal behavior. Black bear dispersal is similar to that of grizzly bears, but the distances are smaller.

High-volume roads like the Trans-Canada Highway near Banff are a barrier to grizzly bears but not to black bears. Grizzlies avoid underpasses, but black bears use them (Woods and Munro 1996). The only effective barriers to grizzly dispersal (other than very large bodies of water) are products of human activities (Craighead and Vyse 1996). Although grizzlies are capable of long-distance dispersal, none of 460 radio-tagged grizzlies have traveled between the large core reserves in the northern Rockies within the past twenty-five years (Servheen personal communication, reported in Weaver et al. 1996). It is likely that barriers produced by human activities have impeded these longer movements, for grizzlies in contiguous habitat unaltered by humans often travel this far.

Population sizes, home ranges, and inferences of genetic structure. Recent estimates of grizzly numbers in the GYE include minimums of 133 and 245, an estimate of 390 using marked females, an estimate of 339 based on distinct families, a bootstrapped estimate of 344 with a 90 percent confidence interval of 280–610, and an interagency population review committee estimate of a minimum of 245 bears, of which sixty-seven are adult females (Eberhardt and Knight 1996). However, an estimate of N_e for the Yellowstone population is only thirteen to sixty-five effective grizzly bears (Paetkau et al. 1997). Female grizzly home ranges vary greatly in size (Craighead et al. 1995), ranging in the GYE from 233 square kilometers for males and seventy-three square kilometers for females (Craighead 1976) to 1,970 square kilometers for males and 874 square kilometers for females (Knight et al. 1984). In the Mission Mountains of Montana home ranges for males averaged 1,403 square kilometers (Servheen 1983). The aver-

age lifetime home range size is about 3,885 square kilometers (Mattson and Reid 1991), but female home ranges average around 450 square kilometers (Merrill personal communication).

In a study of microsatellite alleles in a grizzly population over 5,200 square kilometers in the western Brooks Range, Craighead et al. (1995) found no evidence of a Wahlund effect (deficiency of heterozygotes) and thus no indication of genetic structure. Other larger Arctic study areas also showed no evidence of genetic structure (Paetkau et al. 1997). The Greater Yellowstone Recovery Zone is almost five times as large as the western Brooks Range study area, and the GYE is about eight times as large, so that some genetic structure may once have existed between grizzlies at extreme ends of the ecosystem. Genetic structure is evident today on a larger metapopulation scale between the GYE and populations further north (Paetkau et al. 1997). Grizzlies, like wolves, could disperse between the large core reserves in a single season, but they typically travel shorter distances.

Black bear status and distribution has been given little attention in the GYE. In Montana about one thousand black bears are harvested annually (Montana Department of Fish, Wildlife and Parks 1994). Black bears are found throughout Yellowstone Park, and populations are presumed to be stable. One estimate of five hundred for Yellowstone National Park has been made by the U.S. National Park Service (1989). The status of the population is somewhat uncertain, however, for one estimate of illegal kills was forty black bears in 1991 and 1992. Black bears prefer more heavily forested areas than grizzlies and are more tolerant of human activities. In eastern Alberta, Young and Ruff (1982) found mean home-range size of males to be 119 square kilometers and 19.6 square kilometers for females. In Idaho Amstrup and Beecham (1976) reported home ranges from 109 to 115 square kilometers for males and seventeen to thirty square kilometers for females. In Montana male home ranges were 53 to 225 square kilometers and female home ranges were fourteen to 137 square kilometers (Kasworm and Thier 1991, Aune and Brannon 1987, Greer 1987). It is likely that slight genetic subdivision exists at the scale of the entire GYE. Because of black bears' cover and security requirements, immigration from distant populations is restricted to the same routes that grizzly bears use.

FELIDAE: BOBCATS, LYNX, AND MOUNTAIN LIONS

The Felidae have also received little attention in the GYE. Mountain lions have been studied only during the last decade as they have returned to the Northern Range following their virtual extirpation earlier in the century.

Current genetic research. Little genetic research has been done to date on the Felidae that inhabit the GYE. Microsatellite DNA analysis of mountain lions has

revealed paternity of cubs and provides a baseline of allele frequency data and heterozygosity (Murphy personal communication). An ecological study of lynx in northwestern Montana is currently investigating lynx population genetics through the use of microsatellite DNA analysis of hairs collected from scent-rubbing posts (Weaver personal communication).

Patterns of dispersal. Felids are polygynous and polyandrous. Dispersal patterns in mountain lions, bobcats, and lynx also follow the general mammalian pattern, with male dispersers traveling farther. Young female mountain lions tend to remain near their maternal home ranges (Ross and Jalkotzy 1992), but males travel farther and have been known to move up to 480 kilometers (Logan et al. 1986). Female lynx offspring usually remain near their mothers' home ranges, while juvenile males tend to disperse (Koehler and Aubry 1994). When prey are scarce, even resident adult lynx may move long distances. Record distances include 1,100 kilometers and 700 kilometers in the Yukon (Ward and Krebs 1985) and 325 kilometers in western Montana (Brainerd 1985). Six male juvenile bobcats in British Columbia exhibited long-distance dispersal movements (a mean of 109 kilometers), while three juvenile females did not. Males actually traveled at least twice this distance before settling down (Apps 1996).

Population sizes, home ranges, and inferences of genetic structure. Mountain lion home ranges averaged forty-five square kilometers in Wyoming (Logan et al. 1986). Murphy et al. (1991) found lifetime home ranges of 117 square kilometers for females and 889 square kilometers for males in a northern Yellowstone study area. Winter home ranges were smaller. In central Montana Williams (1992) found female ranges of fifty-eight square kilometers and male ranges of 199 square kilometers. In Idaho, Seidensticker et al. (1973) found mean home ranges of 453 square kilometers for males and 268 square kilometers for females. Mountain lions were thought to have been completely eradicated by predator control programs in Yellowstone National Park: one hundred twenty-one had been removed by 1925 (Harting and Glick 1994). Since ecological studies began in the Northern Range in the 1980s, the population appears to be increasing. In Montana 424 lions were harvested in 1993, and fifty-four non-hunting mortalities were reported (Montana Department of Fish, Wildlife, and Parks 1995). Approximately 500 lions were harvested in 1998 (Williams personal communication). Mountain lion distribution is probably restricted by the availability of winter prey. This may act to isolate populations to some degree within the ecosystem, but genetic differences between areas would be ameliorated by gene flow. Cougars can easily disperse to distant areas within the ecosystem or to other ecosystems (all within three hundred kilometers) provided that human activities are not significant barriers to dispersal.

Lynx have been sighted in both Yellowstone and Grand Teton national parks and in the Centennial, Wind River, Gros Ventre, and Absaroka ranges (Harting and Glick 1994). The GYE is near the southern limit of their known range. Although records of lynx occur farther south, it is possible that these were not stable populations (Koehler and Aubry 1994). A population in the Wyoming Range, south of Jackson, is currently being studied by the Wyoming Department of Game and Fish. Lynx populations and their major prey, hares, do not cycle dramatically in the western United States as they do farther north. Populations of lynx in the northern Rockies are therefore relatively stable, perhaps because other predators (coyotes, bobcats, red foxes, hawks, and owls) and competitors help stabilize hare populations (Wolff 1982). Home-range sizes vary greatly with prey abundance but may range from one hundred to three hundred square kilometers in the GYE.

Male bobcats also have larger home ranges than females, according to most studies. In western Montana, Brainerd (1985) found males to average 122 square kilometers, while females averaged 43.1 square kilometers ($N = 17$). In British Columbia males averaged 138.5 square kilometers, while females averaged 55.7 square kilometers. The size of individual home ranges fluctuates with the prey base. When lagomorph numbers are low, bobcats must utilize larger areas. Habitat is chosen to minimize snow depth and energetic expenditure and to maximize hunting opportunities (Koehler and Hornocker 1989, Litvaitis et al. 1986). Koehler and Hornocker (1989) found that rocky terrain was a factor in resource partitioning between bobcats and coyotes, and it also provides security and escape habitat (Apps 1996). Bobcat numbers are probably sufficient for long-term stability in the GYE, but winter habitat and competition with other predators may be limiting and probably isolate bobcat populations somewhat into habitat surrounding the high central Yellowstone Plateau. These patterns of distribution probably contribute to genetic structure, but this has not yet been examined. Bobcats disperse on the order of one hundred kilometers and thus may exhibit some degree of genetic subdivision between extreme ends of the ecosystem. Some genetic structure almost certainly exists between ecosystems.

MUSTELIDAE: WEASELS, SKUNKS, BADGERS, MARTEN, FISHERS,
OTTERS, AND WOLVERINES

Marten are the only mustelids in the GYE for which there is much genetic data available. Wolverines are low in number but disperse widely, which should maintain gene flow. Fishers are low in number and populations are widely separated, which should result in more genetic structure. Otters are low in number and restricted in distribution. The other species should have large

enough populations over a large enough area to capture a degree of genetic structure.

Current genetic research. Mitton and Raphael (1990) examined allozyme variability in a marten population in the central Rocky Mountains. They found very high levels of mean multilocus heterozygosity (0.17) compared with carnivores in general (0.01, summarized by Kilpatrick et al. 1986). However, their sample size of ten was very small. Steven Fain at the National Fish and Wildlife Forensic Lab has developed multilocus DNA fingerprints of martens (Fain personal communication). Researchers at San Francisco State have examined D-loop sequences of mtDNA in California martens with much variation and in fishers with no variation (Zielinski personal communication).

Patterns of dispersal. Mustelids in general disperse as expected. Wolverine subadult females generally remain near their mothers, while males disperse when they reach sexual maturity at two years of age. Two dispersing males each traveled about two hundred kilometers and established home ranges. Two others dispersed and then returned to the natal area (Copeland 1996). A male wolverine in British Columbia dispersed sixty kilometers in ten days (Krebs personal communication). Wolverines do not seem to be deterred by such topographic features as mountains, lakes, and rivers (Hornocker and Hash 1981), but they avoid human developments, extensive settlements, and major access routes (Banci 1987, Ruggiero et al. 1994). In these respects they are similar to grizzly bears. One of the longest wolverine dispersals on record was 328 kilometers from south-central Alaska to the Yukon over about eight months (Gardner et al. 1986). Female fisher home ranges often overlap, and males disperse farther. One male traveled one hundred kilometers, crossing some fairly large open areas in Alberta. Fishers commonly cross one to two kilometers of open areas between woodlots at night (Badry personal communication). Two male fishers in Idaho dispersed twenty-six kilometers and forty-two kilometers (Buck et al. 1983). After reintroductions, fishers often move long distances, ranging from about forty to 163 kilometers from their release sites (summarized in Ruggiero et al. 1994).

Population sizes, home ranges, and inferences of genetic structure. Home-range sizes reported for wolverines averaged 1,522 square kilometers for males and 384 square kilometers for females in Idaho. Male home ranges overlapped about 16 percent, while females overlapped less than 8 percent. Male ranges often include two or three female home ranges (Copeland 1996). In northwestern Montana, Hornocker and Hash (1981) found a mean of 422 square kilometers for male home ranges and 388 square kilometers for females. Copeland reported an average density of one wolverine per 198 square kilometers of habitat. This translates to a maximum of 225 in the GYE, but the number may be

much lower than that, because much of the area is not optimal habitat. Houston (1978) reported twenty-seven wolverine sightings around Yellowstone Park from 1970 to 1978, and Hoak et al. (1982) reported fifty sightings farther south in Wyoming since the 1950s. Given these low numbers and high mobility, it is unlikely that much historic genetic subdivision existed within the GYE, although human-caused fragmentation of habitat may currently be isolating some regions from others. Some genetic differences almost certainly exist between GYE populations and those in other ecosystems, but whether or not these are ecologically important remains to be seen.

A fisher habitat suitability model developed in British Columbia assumes that 259 square kilometers of contiguous habitat are required for transplant attempts. Winter cover is the limiting factor, and road densities need to be very low (Apps 1996). Fishers avoid areas closer than two hundred to five hundred meters from roads and areas over one thousand meters from water (Badry personal communication). In general male fishers require about forty square kilometers of habitat and females fifteen square kilometers (Aubry personal communication). There appears to be a healthy population of fishers in the Bitterroot Mountains in Montana (Foresman personal communication) but very few in the GYE. Powell and Zielinski estimated that two thousand square kilometers of suitable habitat would maintain a population of fifty fishers in the Rocky Mountains (based on Jones 1991). Fisher populations in the GYE may be subdivided into two areas: the northeastern corner of the ecosystem in the Shoshone National Forest and the southwestern corner of Yellowstone Park and the Targhee National Forest (Crabtree personal communication). There are likely genetic differences between these population centers because of the distance apart and the small population sizes.

Marten male home-range sizes averaged about 0.8 square kilometers in Montana (Burnett 1981). Marten and weasel populations appear to be large enough in the GYE to be self-sustaining with adequate levels of genetic diversity, although little genetic work has been completed. There is probably important genetic subdivision across the ecosystem between distant areas such as the Wind River Range, the Beartooth Plateau, and the Madison Range.

Badger home ranges averaged 1.4 square kilometers for males and 1.2 square kilometers for females in southwestern Idaho (Messick and Hornocker 1981). In the GYE, where prey species are less dense, badger home ranges are probably much larger. Severe winters and dense snowpack, plus the lack of open habitat, probably limit badger numbers and distribution greatly in the central part of the ecosystem, the Yellowstone Plateau.

Otters prefer valley habitats over mountain lakes and streams, with use of large valleys predominant. They prefer open-water stream channels during

winter (Melquist 1981). Otter populations appear stable along the main stem of major Montana rivers, such as the Jefferson, Madison, Gallatin, and Big Hole (Zackheim 1982). Extremely cold winter conditions with few open water stretches, coupled with the small size of many GYE headwater streams, probably limits the otter population in the central part of the ecosystem. The headwaters regions will likely be "rescued" by dispersal of individuals from source populations in the downstream reaches as long as those sections retain good otter habitat. Because otters are restricted primarily to riparian habitats, populations in the tributaries of the larger drainages may be genetically subdivided, much as fish stocks are, but much less distinctly.

In summary, it is likely that genetic subdivision of the GYE populations of all the medium- to small-sized species is present, particularly because habitat features such as large open areas like the larger valleys are barriers to the forest-dwelling carnivores. The larger lakes and rivers may hinder dispersal of most species during peak dispersal times in spring and fall. Upland areas, of course, act as barriers to riparian species such as mink and otters and perhaps even fishers.

GENETIC IMPLICATIONS FOR CARNIVORE MANAGEMENT

Species such as carnivores that require large areas of habitat can maintain only small populations on the Greater Yellowstone "island." It is estimated that the amount of habitat to support a grizzly bear, for example, ranges from 450–900 square kilometers. The number of breeding females fluctuates around fifty, but the effective breeding size appears to be in the range of thirteen to sixty-five (Paetkau et al. 1997).

Initial estimates suggest that the carrying capacity for wolves in Yellowstone Park (ten packs or one hundred animals) is close to being reached. The limiting factor is winter range for prey species and the tolerance of sympatric humans. Yellowstone Park will support only as many wolves as can survive through the winter. As wolves expand south, however, the Jackson Hole valley, with its wintering elk herd, should support many more. The first dispersing wolves observed ($N = 9$) reached this area in January 1999. With their great mobility, wolves in the GYE will soon be augmented by dispersers from the other core reserves.

Similarly, the population size of mountain lions is also limited by winter range and human attitudes: within the park this is essentially the Lamar-Gardiner valleys and the larger geyser basins. Prey species flourish at lower elevations around the perimeter of the ecosystem, but those areas are being populated by humans.

Wolverines can adapt to a variety of habitat types but are very sensitive to

human disturbance. They prefer areas with year-round prey in undisturbed wilderness area (Banci 1994). Their denning habitat in the Rocky Mountains appears to be limited to high-elevation, rocky cirques (Koehler 1996). Denning habitat and the distribution of prey limit wolverine population size.

Lynx prefer boreal forest above about 1,900 meters in elevation, particularly early successional stages with high numbers of snowshoe hares and other prey (Koehler and Aubry 1994). Fishers prefer late-successional coniferous forests with high densities of snowshoe hare or porcupines (Powell and Zielinski 1994). The GYE is at the southern limit of the distribution of both lynx and fisher, but they are found in habitat connecting the GYE to the NCDE. Prey and habitat availability appear to limit fisher and lynx. River otter population sizes are constrained by the availability of riverine habitat, and otter populations thus will always remain small in the GYE.

It is the larger carnivore species for which genetic stochasticity is most critical: grizzly bear, wolf, wolverine, cougar, lynx, fisher, and otter are the species most at risk. If we can maintain populations of these species within the GYE, by maintaining all the habitat currently available, their population sizes will remain small enough for genetic effects to tip the balance that could lead to extinction. Inbreeding depression effects will always be critical for the species with small populations: the wolf, because of its high growth rate potential, will be affected least and will also benefit from a reintroduction scheme designed to increase genetic diversity.

Genetic diversity is an important concern for the long-term survival and adaptation of all carnivore species. Natural immigration by dispersing individuals from distant populations may serve to rescue declining populations and may represent selective forces and aspects of genetic diversity that human-managed translocation of captured animals ignores. The genetic future of these populations in the Greater Yellowstone, as well as that of other carnivores, is inextricably tied to the effects of human population growth and to human attitudes and values. Specifically, the more that human activities isolate the GYE from other populations (increase the distance to the "mainland") and alter the habitat within the ecosystem (reduce the size of the "island"), the greater the loss of genetic diversity and gene flow.

Summary and Conclusions

Biodiversity is much like the metaphorical Persian carpet from which Quammen (1996) launches his essay on islands and extinction: it is ancient, it is intertwined, and it is intricate. We have examined the genetic level of biodiversity in the GYE's carnivores, but genes empower and guide individuals on whom depend the fate of populations, and success and failure at individual

and population levels feed back to alter gene frequencies. The connections run up and down the levels of biotic complexity, and it is only with our powers of scientific abstraction that we can think of them in isolation. The GYE is not a pristine Persian carpet of biodiversity, an isolated showcase for the ages. By using crude and blunt instruments of habitat alteration, inhibiting carnivore dispersal with ribbons of concrete and gravel, and replacing plant and animal communities with our own kind, modern humanity has torn the GYE from the broader fabric, leaving a tatter of unraveling edges. We must manage insightfully and purposefully to keep this tatter locally whole, locally a representation of the former whole, the colors strong and the details sharp.

The common thread that weaves through the fabric of life, from individual to individual, through populations and species and ancestral life forms, through years and decades and eons, is the genetic code—the abstract pattern book from which all is fashioned. It is a pattern book for species, and over time even the pattern can slowly change. Fundamental changes in the genetic code occur slowly, on an evolutionary time scale, as a response to long-term shifts of environmental factors. However, when the environmental conditions change suddenly, the genetic shift entails a rapid reduction in genetic variability. Further shifts in the environment can leave the species without the variation necessary to fashion adaptive responses.

Genetic diversity underlies the fitness of populations, including the short-term ability to adapt to local changes and the long-term potential to evolve. Each species has a basic genetic blueprint with essential features common to all individuals. Every individual blueprint is unique, however, because of individual variation, which occurs constantly through sexual reproduction and sorting of alleles. Genetic change occurs in every generation as the blueprint is fine-tuned to local environmental conditions through natural selection and through chance events that act to increase or decrease alleles in the population. Genetic change, particularly a reduction in genetic variability, is accelerated in small populations.

Rapid environmental changes are occurring now, reducing the numbers of wildlife populations and individuals. Worldwide habitat changes are reducing genetic diversity and reducing biodiversity. From the viewpoint of many species, human population growth can be considered a catastrophic event. The current catastrophe, however, has resulted from more than just an increase in our numbers. By altering our environment to achieve our own ends, we have drastically altered the environment for many other species as well. As a sentient and perhaps sapient species, we must be conscious of the effects of our actions. We know what we are doing, and we are responsible for the results. The current worldwide destruction of habitat and the wave of extinctions are per-

haps avoidable. In many places on the planet we still have time to preserve habitats, populations, and species, and thus biodiversity. The Greater Yellowstone Ecosystem is one of these special places.

Carnivore populations are especially susceptible to reduced genetic diversity as a consequence of human activities. The GYE is one of the few remaining places with enough intact habitat to maintain stable carnivore populations and to provide for gene flow from one population to another. Grizzly bears, wolves, and wolverines probably need more habitat than is available in currently protected landscapes in the GYE to safeguard genetic diversity and provide a refuge from extinction. Lynx, fishers, and otters require less area, but their habitat and prey in the GYE are restricted, and thus their populations are small and may be genetically subdivided. To remain viable in the GYE, lynx and fishers need to maintain contact with populations and forested habitats farther north. Subpopulations of all carnivore species need to be identified better and their habitats protected. Baseline genetic research on the six species mentioned above is desperately needed. Additional research on other carnivore species is an important next step. Any carnivore that is handled by researchers should be sampled routinely for future genetic studies, including a blood sample if possible or at least a hair sample. Connectedness between subpopulations within the GYE should be a management priority. Human recreation and vehicle traffic should be managed with wildlife movements in mind.

The movement of large carnivores (and thus their genes) in and out of the GYE is restricted. One practical reserve design for these species is to maintain existing habitat connections with other wilderness ecosystems, specifically the Northern Continental Divide and Salmon-Selway ecosystems. The distance to both these large reserves is less than three hundred kilometers (figure 11.2), well within the dispersal range of the larger carnivore species. A network of reserves with connecting corridors is a workable solution. Minimally disturbed habitat sufficient to support small populations currently exists in intermediate locations. These areas are currently occupied by cougars and have historically been occupied by grizzly bears. Many of these areas also support all of the small and medium-sized carnivores.

Most of these islands of habitat, if managed with that goal in mind, could support one or more large carnivore family groups. Gene flow and population rescue could occur for bears, cougars, wolverines, and other species as long as dispersing animals could negotiate the human-altered landscape between islands of habitat. Such dispersal could occur in a single season, or it could take generations. Such obstacles to movement as human transportation corridors could be ameliorated in just a few places to greatly increase the probability of wildlife movement. The GYE could be managed as one population center of a

regional metapopulation; gene flow within the metapopulation would probably increase genetic diversity within each of the component populations (Hedrick 1996, Hedrick and Gilpin 1996). As Doak and Mills (1994) point out, there are difficulties using broad theories such as metapopulation dynamics and island biogeography for conservation planning. One often cited caution is the allocation of scarce or otherwise valuable resources for unproven benefits. The attractiveness of a northern Rockies metapopulation scheme, then, is that most of the reserve connections are already in place and are still roadless and largely undisturbed. We can maintain them in this state and improve connectivity if we want. Thus implementation of reserve designs to maintain carnivores depends on the collective will of the human populations involved. The most significant variable affecting carnivore persistence may well be public opinion, which needs to be responsibly informed. It is our hope that this chapter and this book will help serve that need.

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