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Source: *The Auk*, Apr., 1994, Vol. 111, No. 2 (Apr., 1994), pp. 504-506

Published by: Oxford University Press

Stable URL: http://www.jstor.com/stable/4088620

The Auk 111(2):504–506, 1994

Charadrius montanus— Montane, Grassland, or Bare-ground Plover?

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The Mountain Plover (*Charadrius montanus*) is an aridland member of the Charadriidae. This plover is generally considered an associate of the North American shortgrass prairie, which is dominated by blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*; Graul 1975). The species breeds at many locations across the western Great Plains plus at isolated locales in western Colorado, Wyoming, and New Mexico (Leachman and Osmundson 1990) and recently in eastern Utah (K. S. Day pers. comm.). Continental populations of the Mountain Plover declined 63% from 1966 to 1991 (Knopf 1994), with the historic and current breeding stronghold being the Pawnee National Grassland in Weld County, Colorado (Graul and Webster 1976). Currently, a second major breeding population of Mountain Plovers is on the Charles M. Russell National Wildlife Refuge, Phillips County, Montana. Unlike when found on the grassland landscape of Weld County, Mountain Plovers in Phillips County selectively nest in prairie dog (*Cynomys* spp.) towns (Knowles et al. 1982, Olson and Edge 1985) in vegetative settings that include prickly pear (*Opuntia polyacantha*), fringed sagewort (*Artemisia frigida*), big sagebrush (*A. tridentata*), western wheatgrass (*Agropyron smithii*), and blue grama. Collectively, Weld and Phillips counties provide nesting habitat for approximately one-half of the continental population of Mountain Plovers.

Despite the differences in vegetation associations at the two major nesting locales, both Graul (1975) and Olson and Edge (1985) have described the tendency of plovers to place nests in areas of low herbaceous vegetation, reduced shrub cover, and near prominent objects such as cow-manure piles or similar-sized rocks. However, plover nests on Montana prairie dog towns also occur in areas of approximately 27% bare ground, a descriptor not mentioned by Graul (1975). The bare-ground variable may have some significance in light of recent findings of plovers sometimes nesting on plowed fields (Shackford 1991, pers. comm.) and descriptions of wintering habitats of plovers that mention use of freshly plowed ground in the San Joaquin and Imperial valleys of California (Grinnell and Miller 1944). We used a methodology similar to that employed in the Montana studies to ascertain if nest sites of Mountain Plovers also include a component of bare ground in native habitats on the relatively prairie-dog-free Pawnee National Grassland of Colorado.

The Pawnee National Grassland encompasses 78,130 ha of shortgrass prairie on loamy, clayey, and sandy soils. Historically, the area supported uncountable numbers of bison (*Bison bison*; Frémont 1845, Voorhees 1920, and many accounts in Mattes 1988); hundreds of wallows remain clearly visible and mostly unvegetated. Besides the shortgrasses, common woody plants include prickly pear, yucca (*Yucca* spp.), and rabbitbrush (*Chrysothamnus* spp.).

We located 43 Mountain Plover nests on the Grassland during the 1991 and 1992 breeding seasons. A half-meter (1.0×0.5 m) rectangular frame was centered over each nest in a northwest-to-southeast orientation, after which the site was photographed. Comparison sites (also 0.5 m^2, referred to as "control" sites hereafter) were located by stretching a fiberglass tape oriented to the north for the 1992 nests ($n = 18$), and placing the half-meter frame on the ground in a northwest-to-southeast orientation at marked intervals of 10, 25, and 50 m from the nest. Control sites also were photographed.

During analysis of vegetative cover, a clear dot grid was overlaid on each photograph to estimate the percentage of area in shortgrass vegetation or bare ground. We also recorded frequency of cow-manure piles and prickly-pear plants within each plot.

A Kruskal-Wallis test with a correction factor for tied ranks and chi-square tests (Zar 1984) indicated no differences in percentages of vegetation cover and prickly-pear presence among the 10-, 25-, and 50-m control sites. A chi-square test comparing cow-manure piles in the three groups could not be employed because more than 20% of the expected frequencies were less than 5.0% (observed values in the three groups were 3, 2, and 2, respectively).

Data from control plots ($n = 54$) were combined for comparison with those from nest sites (Table 1). Shortgrass vegetation averaged 86 $\pm$ SD of 11% of the area within those plots, 13% had dried cow-manure piles, and 28% contained prickly pear. Comparing nest sites to the pooled control sites, percentage of vegetative cover was significantly lower ($U = 1931.5$, df = 42 and 53, $Z = 5.59$, $P < 0.001$ in a two-tailed test of normal approximation), and there were more cow manure piles ($X^2 = 12.2$, $P \leq 0.001$) and fewer prickly pears ($X^2 = 11.48$, $P \leq 0.001$) at nest sites.

These data further characterize structural subtleties at nest sites selected by Mountain Plovers and support previous observations that some plovers nest near a conspicuous object. Graul (1975) reported 55% of nests

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TABLE 1. Mean percentage grass cover (±SD) of 0.5-m^2 plots, and percentage of plots with dried cow manure and prickly pear.

Plot	Grass	Dried cow manure	Prickly pear
Nest	68 ± 17	49[a]	7
Control			
10 m	88 ± 10	17	28
25 m	85 ± 11	11	22
50 m	86 ± 11	11	33
Subtotal	86 ± 11	13	28

[a] Includes count of one large flat rock.

located within 30 cm of a manure pile, and Olson and Edge (1985) reported 27% of nests on prairie dog towns were near a rock 8 cm or more in diameter. We observed 49% of plover nests placed near either a manure pile or a rock.

Relative to physical objects near nests, the only contradiction between our data and observations from earlier studies was the lower prickly-pear densities near nest sites on the grasslands. Olson and Edge (1985) saw no difference in prickly-pear densities at nest sites and random sites on prairie dog colonies, but both nest sites and control sites on those prairie dog towns had lower prickly-pear densities than control sites located outside the area impacted by prairie dogs. Sordahl (1991) noted that Mountain Plover chicks also occur at sites of decreased prickly-pear densities on the Pawnee National Grassland.

Graul (1975) speculated that Mountain Plovers nest near a prominent object to make themselves less conspicuous to predators. This hypothesis has been advanced for many plover species (e.g. Haig 1990), but specific tests for any one species are rare (Grover and Knopf 1982). We wonder, however, why manure piles and rocks would reduce predation on nests when the equally sized, structurally more complex, and physically more ominous prickly pear would not be selected for this purpose. The biological (in addition to statistical) significance of why some birds place nests near objects merits further inquiry.

Olson and Edge (1985) reported 27% bare ground at nest sites in Montana, which is similar to the 32% unvegetated area around nests on the Pawnee National Grassland. Four additional observations suggest that 30% bare ground is likely closer to a minimum habitat requirement than an optimal one in Mountain Plover ecology. First, Mountain Plovers nest in the more xeric landscapes west of the shortgrass prairie province. Second, most nesting attempts by plovers on the Pawnee National Grassland are initiated from late April through May (Graul 1975), a period when the shortgrass species remain dormant. Third, plovers often raise broods in the vicinity of excessive, local disturbance as at cattle watering or loafing areas. Fourth, Mountain Plovers definitely winter, and occasionally nest and raise chicks, on plowed ground.

Since first collected by J. K. Townsend (1839) near the Sweetwater River (Wyoming), the name of the Mountain Plover has always been considered a misnomer in that the species does not actually occur in montane settings. Rather, most field biologists think of it as either the "you-can-see-the-mountains-from-here" plover or the "prairie" plover. Based on the constancy of bare ground across habitats within the annual cycle of the Mountain Plover, and its former cohabitation with 30 million bison (Roe 1951) and even more prairie dogs (Marsh 1984) on the western Great Plains, we offer that this species is a disturbed-prairie or semidesert species rather than a specific associate of grassland, an interpretation that brings the species more in accord with the bare-ground habitat preferences of other charadriids.

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Received 30 March 1993, accepted 2 July 1993.

DATE OF ISSUE (Vol. 111, No. 2): 19 May 1994

7. SELECTION AND DRIFT IN METAPOPULATIONS

Hanski and Gaggiotti, by Michael C. Whitlock

7.1 INTRODUCTION

The distribution of a species over space has many interesting and important evolutionary consequences. All of the basic population genetic forces — drift, selection, migration, mutation, and recombination — act differently in a spatially structured population. Genetic drift can be enhanced or diminished relative to a panmictic population of the same total size. Selection can be more or less effective. Migration is impossible without a spatial context; the consequences of mutations tend to be lowered, and the effective recombination rate is reduced. This chapter reviews some of the effects of population structure, in particular focusing on how selection and drift are changed by the fact that species exist in space. This chapter takes a heuristic and largely nonmathematical look at these issues, trying to express intuitively some recent results in spatial population genetics. This chapter focuses on the dynamics of a single locus, whereas the topics of multilocus selection and quantitative genetics are discussed in Chapters 9, 11, and 12.

One very important summary statistic about the effects of population structure turns out to be one of the oldest: Wright's F_{ST}. There are several ways to define F_{ST}, but they all are standardized measures of the genetic differentiation among populations. Here let us define F_{ST} as the variance in allele frequencies across populations (V_{among}), standardized by the mean allele frequency ($\bar{p}$): $F_{ST} = V_{\text{among}}/\bar{p}(1 - \bar{p})$. F_{ST} has several key features that make

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it useful and interesting for the study of evolution in structured populations. First, F_{ST} has the same expectation for all neutral autosomal loci, although even neutral loci can vary substantially around this expectation. Moreover, this expectation is determined by the demographic properties of the species, such as migration rates, local population sizes, and geography F_{ST} can therefore encapsulate a lot of useful information about the demographic history of a species. F_{ST} tends to be larger if local populations are not connected by high rates of migration and/or if local population sizes are small. Finally, F_{ST} is readily measurable from easily obtained data on real populations, and there is already a lot of information about F_{ST} in nature.

There are other useful ways to view the information conveyed by F_{ST} beyond its use as a measure of genetic variance among populations. F_{ST} is also an indication of the amount of relatedness among individuals in the same demes. If F_{ST} is high, then individuals in the same demes are highly related to one another; in other words, they share many alleles. All else being equal, this also pertains to alleles within a diploid individual: if F_{ST} is high, individuals are more likely to be homozygous than would be predicted by Hardy–Weinberg frequencies. These various interpretations and implications of F_{ST} are useful in interpreting the results that follow. It turns out that because F_{ST} represents both the relatedness of individuals within a deme and the excess homozygosity, it is often the only extra parameter needed to describe how population structure changes the pace of evolution.

This chapter reviews the effects of spatial population structure on the amount of genetic drift and the response to selection. The greater part of the chapter then uses these results to discuss basic evolutionary genetic quantities in structured populations, such as the balance point between mutation and selection, mutation load, inbreeding depression, the probability of fixation of new alleles, and other basic quantities. It turns out that these fundamental evolutionary processes are sometimes strongly affected by even a weak population structure.

7.2 GENE FREQUENCY CHANGE IN METAPOPULATIONS

Gene frequency can change in a species by four mechanisms: selection, drift, introgression from other species, and mutation. This section reviews mathematical models that show the effect of population structure in the two more important of these forces, selection and drift.

Genetic Drift

Genetic drift is the change in allele frequency from one generation to the next caused by random sampling of alleles. Genetic drift is nondirectional, meaning that the average change due to drift is zero, but as the population size gets small, the actual change in allele frequency in any given generation can be relatively large.

Effective Population Size

The smaller the effective population size, the more random effects can become important. A key term here is "effective" — the actual amount of genetic drift in a population is determined not only by the actual number of individuals in the population, but also by other factors, such as the distribution of reproductive success in the species. The *effective size*, N_e, of a population is defined as the size of an ideal population, which would be expected to have the same amount of genetic drift as the population in question. An *ideal population* is one in which each of the alleles in the offspring generation have an equal and independent chance of having come from each of the parental alleles. An ideal population would function as though each parent allele contributes an equal and large number of copies to a gamete pool, and then offspring would be formed by random draws from this gamete pool.

Real populations are not ideal though for several reasons. First, and most importantly, in real populations, each individual is not expected to contribute equally to the next generation: some are very fit and have a high reproductive success, whereas others die before even reproducing. This variance in reproductive success tends to reduce the effective population size and therefore increase the rate of genetic drift. Second, in real populations, new individuals are not necessarily formed at random from the available alleles. For example, with inbreeding, individuals are formed with a higher than random chance of having similar alleles at homologous sites. Such inbreeding tends to decrease N_e because each individual effectively carries fewer copies of alleles. Finally, both variation in reproductive success and nonrandom mating can be inherited across generations, and the correlations in reproductive success which result can also affect N_e.

In structured populations, these three factors are even more important. When organisms live in different places, they are likely to experience different conditions, and therefore there is likely to be greater variance in reproductive success than in a single well-mixed population. Population structure causes a kind of inbreeding because locally mating individuals are likely to be related. Finally, if local conditions are correlated positively from one generation to the next, variance in reproductive success will also be correlated among parents and offspring, assuming limited migration.

The effective size of structured populations has been well reviewed by Wang and Caballero (1999).

The Island Model

Describing the effective size of subdivided populations has a long history, beginning with Sewall Wright in 1939. In this paper, Wright derives the effective population size of a species subdivided by an island model, finding it to be

$$N_{e,Island\ Model} = \frac{Nd}{1-F_{ST}}, \tag{7.1}$$

where N is the number of individuals in a deme, d is the number of demes, and F_{ST} is given, for large d at equilibrium, by

$$F_{ST,Island\ Model} \cong \frac{1}{4Nm+1}. \tag{7.2}$$

Here, m is the migration rate among demes. In the island model, each deme contributes a proportion m of its individuals to a migrant pool and then receives the same number of migrants chosen randomly from that migrant pool. It is important to note that these are not random proportions, but that each deme gives and receives exactly Nm individuals to and from the migrant pool each generation, and each deme consists of exactly N individuals. As a result, each deme contributes exactly equally to the next generation. This seemingly innocuous assumption turns out to have fairly important effects on interpreting results obtained from the island model.

If each deme contributes exactly equally to the next generation, then there is no variance in reproductive success among demes. We know from classical population genetics that a lower variance in reproductive success means higher N_e, and in fact this is the case with structured populations as well. Look again at Eq. (7.1). Give that F_{ST} is a quantity that ranges between 0 and 1, the N_e for an island model is always something greater than Nd, in other words greater than the total number of individuals in the metapopulation as a whole. This is because of the assumption that there is no variance among demes in reproductive success.

Relaxing Island Model Assumptions

A more general model of the effective size of structured populations has been derived (Whitlock and Barton, 1997). The general form of the equation for N_e in a species that has reached demographic equilibrium is given by

$$N_e = \frac{\overline{N}d}{\sum_i \frac{N_i w_i^2 (1 - F_{ST,i})}{\overline{N}d} + 2 \sum_i \sum_j \frac{w_i w_j N_i N_j \rho_{ij}}{\overline{N}d}} \tag{7.3}$$

where N_e is shown to be a function of the local population sizes (N_i), the relative contributions of each deme (w_i), the F_{ST} predicted over a set of demes with demographic properties such as deme i ($F_{ST,i}$), and the correlation among demes of allelic identity (ρ_{ij}, which is defined similar to F_{ST}, but instead using covariance of pairs of demes). This equation makes few assumptions about the nature of the spatial subdivision among populations, allowing for variable migration rates over different population pairs, including isolation by distance, local changes in population size, including local extinction, and new population formation via colonization or fission.

While general, Eq. (7.3) is a bit unwieldy for intuitive use. To aid in explaining a few key features of this result, let us use a simplified version of this equation that makes a few more assumptions. If all demes have the same size as each other, but contribute unequally to the next generation via differential migration, then we can write V as the variance among demes in the expected reproductive success of individuals from that deme (i.e., $V = \mathrm{Var}[w_i]$). The effective population size is then

$$N_e = \frac{Nd}{(1 + V)(1 - F_{ST}) + 2NF_{ST}Vd/(d - 1)} \tag{7.4}$$

(Whitlock and Barton, 1997).

Let us examine two extremes using Eq. (7.4). If, as in the traditional island model, the variance among demes in reproductive success is zero, then Eq. (7.4) reduces to Eq. (7.1) [This is true not only for the island model, but for any model for which each deme is equal in size and contributes exactly equally to all other demes, provided that all demes are ultimately reachable by each deme via migration (Nagylaki, 1982). This includes classic stepping stone models.]

At the other extreme though, let us imagine that one deme is extremely successful and produces all of the offspring that fill all d of the demes. In this case, we would intuitively predict that the effective population size of the whole system should be the same as the size of the single successful deme, and Eq. (7.4), with appropriate modification, shows us that this is in fact the case. (In this extreme, the F_{ST} would be zero and the variance among demes of allelic reproductive success would be $d - 1$.) This extreme example tells us that N_e can be much smaller than the census size with population structure.

The truth obviously lies somewhere in the middle. It turns out that the boundary between whether population structure increases or decreases N_e is approximately whether or not demes have greater or less variance in reproductive success than would be expected by a Poisson distribution. In other words, if demic structure acts to increase variance in reproductive success relative to that expected by chance, N_e would be reduced. Only if the effects of population structure are to reduce the variance among demes in reproductive success to less than random would N_e be increased. This is perhaps biologically unlikely, yet this is the requirement for the results from the simple island model to hold qualitatively. In real species, the opposite is likely to be true: different demes are likely to have different amounts of resources, and different demes are likely to experience different levels of other ecological factors that might affect success, such as levels of parasitism, disease, predation, weather fluctuations, and other catastrophes. Realistic ecology implies higher than random variance among demes in reproductive success, and therefore the effective size of a subdivided species is likely to be reduced, perhaps substantially. The island model is not a good descriptor of typical population structure, for this and many other reasons (see Whitlock and McCauley, 1999).

Extinction and Colonization

It will be useful to consider a couple of specific cases that go beyond the simple island model. One aspect of population structure that has attracted some attention is the possibility of local extinction and recolonization (Slatkin, 1977; Maruyama and Kimura, 1980; Whitlock and Barton, 1997). The models considered in these papers are similar: the basic structure is like an island model, except that each deme has some chance per generation of going extinct independently of its genotype frequencies. An equal number of new demes are colonized, either in the same places recently vacated by the extinction events or in other vacant sites, by a small number of individuals. As a major, unrealistic simplification, each new deme then immediately grows back to N individuals, like all other demes.

With local extinction and recolonization, population structure contributes in an obvious way to the variance in reproductive success among demes. Even though this model is based on the island model, even a small rate of extinction is enough to cause the effective population size of the species to be reduced rather than increased. The main reason is perhaps obvious: with extinction and recolonization, some demes have zero reproductive success,

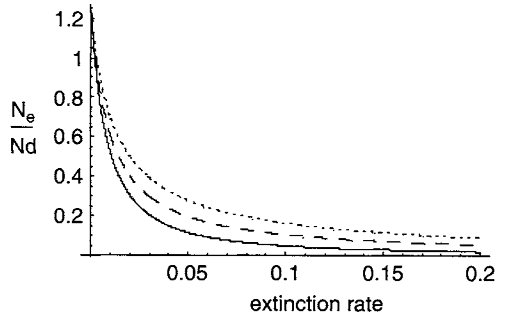

Fig. 7.1 The effective size (displayed as a proportion of the census size) of a metapopulation with local extinction and colonization. Here each deme has 100 individuals, and each new population is founded by four individuals. These colonists have a probability ϕ that they come from the same source population, with $\phi = 0$ in the dotted line, $\phi = 1/2$ in the dashed line, and $\phi = 1$ in the solid line. The migration rate was 0.01 in all examples. As the local extinction rate increases, the effective population size is reduced greatly.

whereas others — those that manage to survive and send colonists to start new demes — have a reproductive jackpot. Thus there is a great deal of variance among demes in reproductive success, which causes the effective size to be reduced. This reduction can be extreme (Fig. 7.1).

Sources and Sinks

In some species, some populations have large amounts of resources, whereas others have so few that they cannot replace themselves without migration (Pulliam, 1988; Dias, 1996; Holt and Gaines, 1992). These so-called "sources" and "sinks," respectively, cause the population dynamics to be different from the island model: demes do not contribute equally to the migrant pool, and therefore there is variance in reproductive success. If the quality of patches of resource is correlated positively over time, then the effect on N_e is even more extreme.

The effects of source–sink structure and correlation over time in patch suitability can be best seen by another extreme example. Imagine that a fraction of demes, say 20%, reside in productive source patches, and the other 80% of demes are what Bob Holt has called "black-hole" sinks — that is, these demes never contribute migrants to other demes and only persist because of migration from source populations. In this case, it is clear that only alleles in individuals in source populations can contribute to future generations and so the only individuals that matter to the evolution of the species are in the source populations. Therefore the N_e of the species should reflect only the effective size of the source populations alone. Thus the N_e of this species should be only 20% of what it would have been with equal migration.

To be more general, we can apply useful results from Nagylaki (1982), who showed that the N_e of a system of populations with a constant migration matrix could be described with the left eigenvector of that matrix. (This assumes a few technical details, such that all demes are ultimately reachable by migration from all other demes, even if it takes multiple steps.) Consider a case where migration is via a migrant pool so all emigrants from all demes are

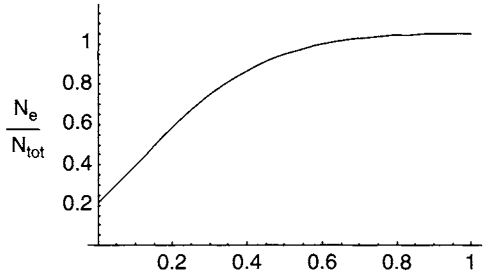

Fig. 7.2 The effective size of a species in which 20% of the demes are sources and the rest are sinks. The *x* axis varies the contribution of the sink populations, expressed as a fraction of the contribution of the sources. Here each 100 demes have 100 individuals, and each receives five immigrants per generation sampled from the migrant pool. As the contribution of sinks reaches zero, the effective size of the system is the same as an island model with only the 20 source populations.

mixed together and then moved on to recipient demes at random with respect to where they originate. Source demes contribute a large number to the migrant pool, whereas "sink" demes contribute a fraction of that number. For simplicity, each deme receives a constant number of immigrants from the migrant pool. This ensures that the F_{ST} among sources and among sinks are approximately equal. Figure 7.2 shows the effective size of these systems as a function of the relative contribution to the migrant pool by sinks. [To make the calculations in Fig. 7.2, Nagylaki's (1982) results were used, accounting for the fact that Nagylaki's definition of N_e differs from the usage here. Nagylaki calculates the N_e that would give the same amount of variance *within* a deme at mutation–migration–drift balance; in other work including in this chapter N_e predicts the amount of variance predicted by the average allele frequency of the species as a whole. The second of these two quantities can be found from the first by dividing by 1-F_{ST}. Details are given in Whitlock (2003).]

Note that with this form of source–sink structure, the effective size of the species is just the effective size of just the source populations when the sinks do not contribute to the future, and it reduces to the island model results when "sinks" contribute equally to sources.

Selection

With good reason, the study of selection in subdivided populations has, in the past, focused on the effects of spatially heterogeneous selection (e.g., Felsenstein, 1976). A great deal of important and interesting evolutionary biology results from variation in selection over space, but population structure, perhaps surprisingly, has a lot of interesting effects even on uniform selection. Arguably, most loci have approximately similar selection in different demes, even though the more obvious and more polymorphic cases may reflect spatially divergent selection. This chapter focuses on this special case in which genotypes have the same relative fitness in each population of the species.

When selection is uniform across populations, it becomes possible to follow the state of the metapopulation by following the mean allele frequency across all local populations, $\bar{q}$. Consider simple selection between two alleles at the same locus, with the fitnesses of the three genotypes given by $1 : 1 + h\,s : 1 + s$. In this case, the change in allele frequency due to selection within each population is a third-order function of q; therefore, to understand how the mean allele frequency would change by selection requires knowing the expected values of q, q^2, and q^3. Fortunately, under most circumstances the dynamics of the expected value of q^3 can be well enough predicted by an understanding of changes in the first two, which reduces the problem to understanding $\bar{q}$ and $E[q^2]$. The expected value of q^2 may seem like an exotic quantity to keep track of, but remember that the variance among demes is derived easily from $\bar{q}$ and $E[q^2]$, and F_{ST} is derived easily from the variance in allele frequency and $\bar{q}$. Thus, a very good understanding of the change in allele frequency across a metapopulation can be obtained by knowing $\bar{q}$ and F_{ST}. Moreover, as long as the selection coefficient is not much greater than the rate of migration into a deme, the F_{ST} predicted from neutral theory works extremely well to predict allele frequency change in structured populations. These conclusions are derived and discussed in greater detail in Whitlock (2002).

[One technical note is necessary: when calculating these quantities, it is essential to weight each individual equally. The usual calculations of F_{ST} weight each local population equally, independent of size. Most models of population structure have assumed equal deme sizes, and therefore they predict the right quantity. Most empirical measures do not measure the appropriate F_{ST} exactly. This may be an important issue in some cases; for example, if smaller demes have higher extinction rates, then the subset of the population with the highest F_{ST}'s would properly be weighted least.]

It will help to look at the equation for the change in mean allele frequency due to selection. From Whitlock (2002), we get

$$\Delta_s\bar{q} \cong \bar{p}\,\bar{q}\,s(1 - r)(F_{ST} + (1 - F_{ST})(h(1 - 2\bar{q}) + \bar{q})) \tag{7.5}$$

where r is the relatedness of two random individuals competing for resources.

Let us consider the various parts of this equation in turn. First, we see that the response to selection is a function of the mean allele frequencies and the strength of selection $\bar{p}\,\bar{q}\,s$. These are the classic terms that would appear even without population structure: the response to selection is proportional to the allelic variance $\bar{p}\,\bar{q}$ and to the strength of selection.

Next, we find that the response to selection is proportional to one minus the relatedness of competing individuals. This last phrase deserves some explanation. Consider a classic dichotomy introduced by Dempster (1955; see also Christensen, 1975) between local and global competition for resources, i.e., soft versus hard selection. With soft selection, each deme contributes a number of individuals to the next generation (whether via resident individuals or migrants) *independent* of the genotypes of the deme. With hard selection, each deme contributes to the next generation in proportion to its mean fitness determined by its genotype distribution. Under soft selection, individuals are competing locally for resources, and therefore there is competition between relatives. The mean relatedness of individuals from the same deme (without inbreeding within demes) is given by $r \equiv 2F_{ST}/(1 + F_{ST})$. At the other extreme, under hard selection, there is no local competition for resources, and the relatedness of competing individuals is zero. Putting these equations into Eq. (7.5), we find that hard selection is always more effective than soft selection in changing allele frequency. With local competition for resources, if an individual does well because of having a good genotype, it will, through competition, reduce the resources available to other individuals in the same deme. With population structure, these other local individuals are likely to share alleles. Therefore the event that would have boosted the number of copies of this good allele in the next generation (the first individual doing well) is partially counterbalanced by competition against the same genotypes.

Note that for the relatedness term, increasing population structure tends to weaken the response to selection. With soft selection, increasing F_{ST} results in greater relatedness and therefore a lower response to selection, *all else being equal.*

Finally, we see in the last term $(F_{ST} + (1 - F_{ST})(h(1 - 2\bar{q}) + \bar{q}))$ a reflection of the effects of increasing homozygosity on the response to selection in structured populations. As F_{ST} increases, so does the proportion of individuals that are homozygous, even for the same mean allele frequency. Greater homozygosity, for the same q, increases the magnitude of the response to selection. This increase is particularly important if $\bar{q}$ is small and the allele is at least partially recessive ($h < 1/2$). In these cases, with panmixia, most alleles appear as heterozygotes and selection therefore cannot discriminate the recessive alleles. As F_{ST} increases, most of the selection is experienced by alleles in the homozygous state, where the alleles have relatively large effects. Thus, in opposition to the effect of relatedness given earlier through its effects on increasing homozygosity, population structure tends to *increase* the response to selection. For nearly recessive alleles, this boost can be extremely large.

This effect of excess homozygosity has been described much earlier with respect to inbreeding within populations (Ohta and Cockerham, 1974). In fact, with hard selection, there is no distinction between the effects of inbreeding due to population structure and that due to local inbreeding; they enter the response to selection equations in exactly the same way. With soft selection, however, the extra effects of competition among relatives change the relationship between F and response to selection.

The balance between these two effects (competition among relatives and homozygosity) depends on the details. With hard selection, there is no effect of relatedness, and population structure therefore always increases the rate of response to uniform selection. With soft selection, response to selection can be either increased or decreased depending on the dominance coefficient of the locus under selection and F_{ST}. The following section shows examples of both. The effects of population structure on even uniform selection are quite complicated.

With this selection equation available, a variety of results on basic selection become easy to derive. The next few sections of this chapter show some of these results.

7.3 MAINTENANCE OF GENETIC VARIATION IN SUBDIVIDED POPULATIONS

One of the oldest questions in population genetics is "what forces are most important in maintaining genetic variation ?" Population subdivision can affect the maintenance of genetic variation in a variety of ways. This section reviews a few of these briefly, focusing on the case of spatially uniform selection.

Mutation–Selection Balance

Estimates have shown that the genomic rate of mutation to deleterious alleles is reasonably high, ranging from a few per thousand individuals to much greater than one per each new individual (Lynch et al., 1999; Keightley and Eyre-Walker, 2000). Although natural selection operates to reduce the frequency of these deleterious alleles, they are not immediately eliminated completely. As a result, some deleterious alleles are always segregating in populations at a frequency determined by the balance between mutation and selection. Some have argued that levels of standing genetic variance observed in natural populations could be explained largely by this mutation–selection balance.

Mutation is likely not much affected by population structure, but the previous section showed that the efficacy of selection can be affected greatly by subdivision. At mutation–selection balance, the deleterious allele is likely to be rare, which simplifies Eq. (7.5) to

$$\Delta_s\bar{q} \cong \bar{q}s(1 - r)(F_{ST} + (1 - F_{ST})h) \tag{7.6}$$

The equilibrium allele frequency at mutation–selection balance is then given by

$$\hat{\bar{q}} \cong \frac{\mu}{-s(1 - r)(F_{ST} + (1 - F_{ST})h)} \tag{7.7}$$

(Remember that in the way we have defined fitness in this chapter, a deleterious allele has $s < 0$.) For recessive alleles in particular, the frequency of deleterious alleles at mutation–selection balance is much reduced with population structure due to the more effective selection against homozygotes. See Fig. 7.3, for some examples. As a result, the amount of variation maintained by mutation selection balance can be reduced greatly in large metapopulations, depending on the distribution of dominance coefficients. Most current estimates of the mean dominance coefficient of mildly deleterious alleles give answers around $h = 0.1$ (Houle et al., 1997; García-Dorado and Caballero, 2000; Peters et al., 2003), so the reduction in variance can be substantial even for relatively small F_{ST} values.

The predominant model of the genetic mechanism for inbreeding depression claims that inbreeding depression results from deleterious recessive alleles segregating in populations at mutation–selection balance. With population structure, the reduction in mean deleterious allele frequency

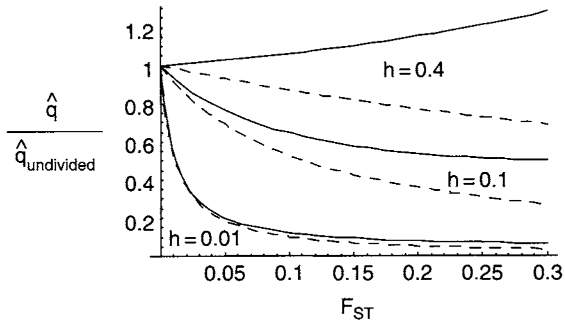

Fig. 7.3 The equilibrium value of the frequency of a deleterious allele can be changed substantially by population structure. Here solid lines indicate pure soft selection and dashed lines indicate pure hard selection. With very recessive alleles, the equilibrium allele frequency is reduced greatly relative to the case in an undivided population (where $\hat{q} \cong -\mu/hs$). Parameter values used for these calculations were $s = -0.1$, $\mu = 10^{-6}$, and the three lines correspond to $h = 0.4$, 0.1, and 0.01 from top to bottom. From Whitlock (2002).

results in a potentially large reduction in the amount of inbreeding depression predicted for a species, even at relatively low F_{ST} values (see Whitlock, 2002).

Balancing Selection

Balancing selection, by definition, occurs when selection acts to increase the frequencies of rare alleles. This can happen with overdominance, negative frequency-dependent selection (where rare alleles are favored because they are rare), or by spatially heterogeneous selection. Each of these are affected by the spatial population structure.

Overdominance

With overdominance, the heterozygote is the most fit genotype. For this section only, let us redefine the fitnesses of the three genotype **AA**, **Aa**, and **aa** as 1-s : 1 : 1-t, such that the fitness of the two homozygote genotypes is reduced by a factor s or t. With overdominance in a large randomly mating population, there is an intermediate equilibrium allele frequency that stably maintains variation in the population as a result of the heterozygote being selected for whenever one or the other of the two alleles becomes too rare.

In structured populations, the extra homozygosity caused by population structure can change the dynamics of the maintenance of variance. Nonrandom mating causes the marginal fitnesses of the two alleles to be determined more by their homozygous effects and less by their effects in heterozygotes. As a result, if the two homozygotes fitnesses are not equal ($s \neq t$), then the allele associated with the fitter homozygote will have a higher frequency than expected under random mating. Mathematically, that frequency is given by

$$\hat{q} \cong \frac{s - tF_{ST}}{(s + t)(1 - F_{ST})}, \tag{7.8}$$

so long as this value is between zero and one, which it need not be (Whitlock, 2002). If F_{ST} is large enough, the expected equilibrium leaves the population fixed for the allele with the most fit homozygote. Thus population structure tends to reduce the amount of variation maintained by overdominance.

Frequency Dependence

In some cases, the fitness function changes with the frequency of alleles in the population or species; this is called frequency-dependent selection. If selection displays negative frequency dependence, then alleles are more fit when rare than when the same allele is common. In this case, selection can act to maintain variation in a population because as alleles get rare (as they would on the path to being lost from the population), their fitness increases and therefore their frequency climbs again.

One of the most studied examples of negative frequency dependence is the self-incompatibility (SI) alleles common to many species of plants. With SI, pollen (or, in some cases, its parent plant) that shares alleles with the maternal plant are not allowed to fertilize ovules. These processes presumably evolved as a mechanism to prevent self-fertilization, but they also prevent unrelated individuals that share alleles from mating. As a result, rare alleles at the SI locus have higher fitness because they are able to mate with more other individuals in the population. All else being equal, the system always favors new alleles being introduced into the population, but real species have limited numbers of SI alleles because of loss due to genetic drift. The smaller the effective population size, the fewer SI alleles maintained at equilibrium.

With population structure, one might imagine that different alleles might be maintained in different populations, thereby increasing the total diversity in the species as a whole. It turns out that this is true for species with very low migration rates between demes, but with realistic, intermediate levels of migration the total number of SI alleles maintained is slightly lower than would be expected with panmixia (Schierup, 1998; Schierup et al., 2000; Muirhead, 2001).

Heterogeneous Selection

It has been known since at least the 1950s that spatially varying selection can maintain genetic variation, especially if there is soft selection (Levene, 1954; Dempster, 1955). The conditions for this are narrower than was commonly thought (Maynard Smith and Hoekstra, 1980), requiring strong, relatively symmetric selection. Felsenstein (1976) and Hedrick (1986; Hedrick et al., 1976) reviewed the theory and empirical evidence for and against the maintenance of genetic variance by heterogeneous selection.

A different form of heterogeneous selection can emerge in populations in which there is already a lot of genetic differentiation among populations. In these cases, epistatic interactions between loci can cause different alleles to be favored locally even when the underlying function describing the relationship between fitness and genotype is uniform across space (see Chapters 9 and 11). This sort of heterogeneous selection depends on there being selectively and epistatically different alleles in different local populations, which becomes important only under extremely restricted gene flow or extreme drift.

One special case of epistasis that may be quite common is that generated on approximately additively interacting alleles that form a phenotype under stabilizing selection. Stabilizing selection causes the fitness effects of alleles to vary depending on whether the sum of the effects of all other alleles in the individual add up to a value above or below the optimum for the trait; hence with stabilizing selection, a population near its optimum will have mainly epistatic variance for fitness associated with that trait (Whitlock et al., 1995). Barton and Whitlock (1997) have shown that with uniform stabilizing selection and low migration, the amount of genetic variance for a trait that can be maintained can be increased substantially as a result of this epistasis. However, this is only likely to be important in species with very high values of F_{ST}, in the range of $F_{ST} > \sim 0.2$.

7.4 ADAPTATION IN SUBDIVIDED POPULATIONS

Population structure can affect the pace of adaptive evolution. We have already discussed the conditions under which the response to selection is increased or decreased with population structure. The subdivision also allows novel patterns of adaptation, such as local adaptation (see Barton, 2001), shifting balance evolution [Wright (1931), but see Coyne et al. (1999) and Whitlock and Phillips (2000)], and more rapid evolution with epistatic interactions (Bryant et al., 1986; Goodnight, 1988; see Chapter 9). More fundamentally though, population structure strongly affects the pace of evolution even for those alleles that are uniformly selected without any complicating interactions with other loci. This section reviews the effects of population structure on the probability of fixation of new mutations.

Probability of Fixation

One of the most remarkable results in population genetics has to be Haldane's (1927) result that a new beneficial allele with heterozygous benefit of hs has only about $2hs$ chance of ultimate fixation. Haldane assumed that the species in question was ideal (i.e., its census size equaled its effective size) and undivided. Even in an infinite population, if a new allele is introduced as only a single copy, the fate of that allele is partially determined by stochastic changes in the numbers of copies of the allele left in each generation. It turns out that by introducing an allele as a single copy (as a rare mutation would likely do), even alleles with moderate selective advantage are more likely to be lost stochastically from the population than fix. Kimura (1964; see also Crow and Kimura, 1970) modified this result to allow for nonideal populations and allowed arbitrary dominance for deleterious alleles as well. He found that the probability of fixation of a beneficial allele is given approximately by $2hsN_e/N$, where N is the census size of the population.

In 1970, Maruyama achieved the first results on the probability of fixation in subdivided populations. He showed that in an island model, the probability of fixation for an additively acting allele was simply s. (For additive alleles, $h = 1/2$, so this result is equivalent to the $2hs$ of Haldane.) Maruyama (1974) and others (Slatkin, 1981; Nagylaki, 1982) extended this result to deal with any model such that each deme contributes exactly equally to the next generation; the probability of fixation with population structure with this restriction remained s. This was viewed by some as an invariant result of population structure; the claim was made that population structure therefore did not affect the probability of fixation of beneficial alleles. However, this conclusion was premature because other models of population structure are possible (and even more reasonable than the island model) and because the effects of dominance were not properly accounted for. The first demonstration that this was not true was a model of extinction and two specific types of recolonization by Barton (1993). In these cases, the probability of fixation was much reduced by population structure relative to the panmictic case.

The probability of fixation in a more general model of structured populations has been found (Whitlock, 2003). Based on Kimura's diffusion equations, this work shows that the probability of fixation can be derived from the equations for drift and response to selection presented earlier in this chapter. Moreover, as long as the strength of selection is lower than the typical immigration rate, the F_{ST} expected for neutral loci can be used in these equations, which expands their usefulness greatly. For dominance coefficients differing from 1/2, the equations cannot be solved directly, but the answers can be obtained with numerical integration. In the interests of space, this chapter will not review the mathematics of the general equations, but will focus on the additive case, as well as an approximation that works very well for beneficial alleles even with arbitrary dominance. More details can be found in Whitlock (2003).

For additive alleles, such that $h = 1/2$, the probability of fixation in structured populations is given by

$$u[q]=\frac{1 - \exp[-2s(1 - F_{ST})N_e q]}{1 - \exp[-2s(1 - F_{ST})N_e]} \tag{7.9}$$

for soft selection and

$$u[q]=\frac{1 - \exp[-2s(1 + F_{ST})N_e q]}{1 - \exp[-2s(1 + F_{ST})N_e]} \tag{7.10}$$

for hard selection, where q is the initial allele frequency of the allele in the metapopulation. If the population starts with a single copy of the new allele, then $q = 1/2N_{tot}$, where N_{tot} is the total size of the metapopulation. These equations look fearsome, but in fact they are quite similar to the equations for the panmictic case derived by Kimura (1964). There are two differences. First, the N_e here is the effective size of a subdivided population, given by Eq. (7.3). Second, the strength of selection s is now modified by a term involving F_{ST}, which reflects the change in the efficacy of selection from population structure.

For beneficial alleles, we can write a simple equation for the probability of fixation of a new mutant, even with arbitrary dominance:

$$u \cong 2s(1 - r)(F_{ST} + (1-F_{ST})h)N_e/N_{tot}. \tag{7.11}$$

Here it is possible to see that this result builds directly on Kimura's. As F_{ST} goes to zero, this approaches the $2hsN_e/N$ given earlier.

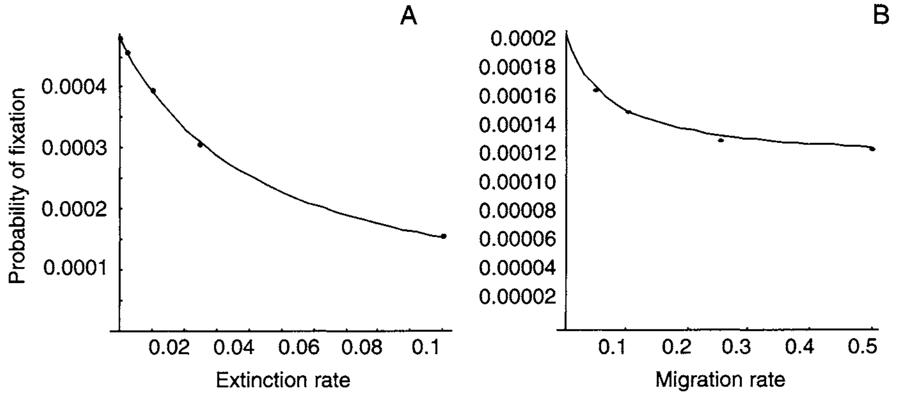

Fig. 7.4 Examples of the fixation probabilities of nearly recessive beneficial alleles (h = 0.01) with soft selection. (A) Extinction and recolonization. In this example, the migration rate between populations was 0.05, colonization occurred by four individuals with a probability of common origin of 1/2, s = 0.002, and there were 100 demes with 100 diploid individuals each. (Each point represents results from 10^7 simulations, so the standard error ranges from 6.9×10^{-6} on the left to 3.9×10^{-6} on the right.) As the extinction rate increases, the effective population size of the metapopulation decreases, and therefore so does the probability of fixation. (B) A one-dimensional stepping-stone model. With a stepping-stone model, F_{ST} (and therefore N_e) increases as the migration rate drops so the probability of fixation also increases with lower migration. This is particularly true with recessive alleles, which are expressed often in the homozygous state with the concomitant increase in the efficacy of selection. (There are 100 demes with 100 diploid individuals each, s = 0.0002 and dots represent 10^6 simulations each.)

These results have been tested by simulation in a wide variety of models of population structure, including the island model, extinction–recolonization, stepping-stone models, and source–sink models. They work remarkably well (see Figs 7.4 and 7.5).

The probability of fixation of beneficial alleles tends to be much reduced with population structure. This is mainly a result of the fact that the effective

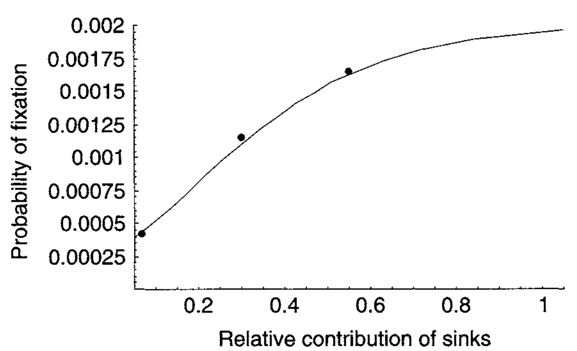

Fig. 7.5 The probability of fixation in a source–sink model. Here there are 100 demes, 20 of which are "sources" and the rest are "sinks". Each deme has 100 individuals, and the immigration rate to the sources is 0.2, whereas it is 0.25 in sinks. Demes exchange migrants by a modified island model, where each sink's contribution to the migrant pool is a fraction of that of each source. As this asymmetry increases, the effective population size is reduced and the probability of fixation of beneficial alleles drops. For these examples, s = 0.002 and h = 1/2, and dots represent results of 10^7 simulations.

population size is reduced in most models of population structure. The probability of fixation can be increased for some loci, especially for nearly recessive alleles that can be expressed more strongly in structured populations because of increased homozygosity.

Let us return to the island model. As mentioned earlier, the island model is an extreme description of population structure because it allows no variance among populations in reproductive success. For additive alleles, Maruyama and successors found the probability of fixation to be simply s in an island model, the same as in an unstructured population. The more general model predicts that the probability of fixation should be $s\,(1 - F_{ST})\,N_e/N_{tot}$ (because the island model in its basic form as used by Maruyama is also a soft selection model). Remember that the island model has the unusual property of having a larger N_e than census size: $N_e = N_{tot}/(1 - F_{ST})$. Putting this N_e into the probability of fixation equation simplifies it to simply s. The results are consistent; what is more important is that the island model is unrealistic and extreme. Most real species will have $N_e < N_{tot}$, and so most will have lower probabilities of fixation of beneficial alleles than predicted by Maruyama's formula. Probabilities of fixation are not invariant with respect to population subdivision.

Relaxing the assumption of uniform selection has been investigated using the island model by a variety of authors (Barton, 1987; Tachida and Iizuka, 1991; Gavrilets and Gibson, 2002). Population structure tends to increase the probability of fixation relative to that expected by the mean fitness of the alleles across demes. It is not yet known what effect heterogeneous selection would have with a more realistic model of subdivision.

Population structure also substantially affects the time taken for fixation of new alleles (Whitlock, 2003).

7.5 GENETIC LOAD IN SUBDIVIDED POPULATIONS

Genetic load is the reduction in the mean fitness of a population relative to an optimal genotype caused by some particular factor, such as deleterious mutation, genetic drift, and segregation (Crow, 1993). Load is sometimes strongly affected by population structure, as reviewed in this section.

Mutation Load

Mutation load is the reduction in mean fitness caused by recurrent deleterious mutations in a population. Mutation load is usually calculated at mutation–selection balance: that is, it is the mean reduction in fitness associated with an allele frequency predicted by the equilibrium between mutation and selection. In panmictic populations, the load associated with an allele that is not completely recessive is $L = 2\mu$ (where μ is the mutation rate from wild type to deleterious allele; remarkably, this is not a function of the strength of selection against the deleterious allele).

With population structure, load equations become more complicated (Whitlock, 2002):

$$L \cong -(2h(1-F_{ST})+F_{ST})s\hat{\bar{q}} \tag{7.12}$$

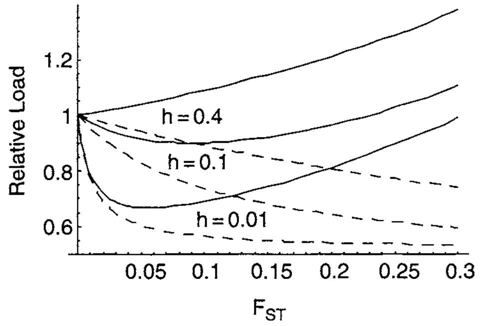

Fig. 7.6 The mutation load in a metapopulation relative to the load at a similar locus in an undivided population (~2μ). For the values of F_{ST} likely to be found within species and relatively small values of the dominance coefficient h, the mutation load can be reduced substantially in a subdivided population. Solid lines show pure soft selection, whereas dashed lines correspond to pure hard selection. Parameters for this example are $s = -0.1$, $\mu = 10^{-6}$, and the three pairs of curves correspond to $h = 0.4$, 0.1, and 0.01 from top to bottom.

where the value of $\hat{\bar{q}}$ is given by Eq. (7.7). Note that s will cancel out when this substitution for $\hat{\bar{q}}$ is made, but load remains a function of the dominance coefficient, unlike the panmictic case. Figure 7.6 shows the change in load as a function of population subdivision. Load is always reduced with hard selection, but with soft selection, load is increased for high values of F_{ST} and near additivity. With nearly recessive alleles, the reduction in load can be nearly 50%.

Segregation Load

Segregation load is the reduction in fitness caused by the inability of a population to be composed entirely of heterozygotes even when these genotypes are the most fit. As such, segregation load requires overdominance. With population structure, there are even fewer heterozygotes in a species than under Hardy–Weinberg conditions so the segregation load would be more pronounced. Using the same notation as in the overdominance section given earlier, the segregation load is expected to be

$$L = \frac{(1 + F_{ST})st}{s + t}, \tag{7.13}$$

which reduces to the segregation load in a panmictic population when $F_{ST} = 0$ (Crow, 1958). Therefore, the segregation load is $(1 + F_{ST})$ times as great in a subdivided population as in an undivided one, as expected by the increased number of homozygotes.

Drift Load

Drift load is the reduction in fitness caused by drift changing allele frequencies away from those favored by selection. An extreme form of drift load results from fixation of deleterious alleles by drift. Drift load has received a lot of attention in the last several years because of the possible mutational meltdown of small endangered populations (Lande, 1994; Lynch et al., 1995a,b).

The rate that deleterious alleles accumulate in a species is a function of the efficacy of selection and of the effective population size; the smaller these two values are the faster drift load will accumulate. We have seen that selection is often more effective in structured populations (although not always), but more importantly, the effective population size tends to be reduced by structure. Because the latter of these two effects turns out numerically to be more important, in most cases, population structure increases the rate of accumulation of deleterious alleles (Higgins and Lynch, 2001; Whitlock, 2003). This is most pronounced in cases with large variance in reproductive success among demes, such as with extinction and recolonization or source–sink models. Figure 7.7 shows that the change in the probability of fixation of deleterious alleles can be reasonably large (two- to three fold), although perhaps in most cases the change is less than a doubling.

Migration Load

If the local population in a deme is well adapted to local conditions and if migrants to this population come from populations adapted to other conditions, then the alleles that come into the population by migration are likely to be poorly adapted to local conditions. The reduction in mean fitness that results is called *migration load.* Migration load increases with increasing differences in the selection coefficients among populations and with migration rate. In some species, migration load is likely to be the most important type of genetic load. Migration load may be key in determining the range limits of species because migration from the species center may prohibit further local adaptation at the margins (Mayr, 1963; Kirkpatrick and Barton, 1997).

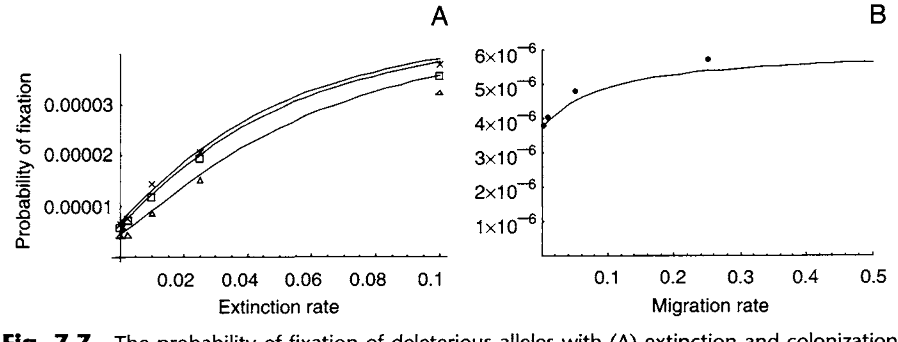

Fig. 7.7 The probability of fixation of deleterious alleles with (A) extinction and colonization or (B) a one-dimensional stepping stone model. (A) The three lines plot, from bottom to top, the predicted probability of fixation for alleles with dominance coefficients of 0.5, 0.1, and 0.01, respectively. The symbols mark simulation results over a minimum of 10^7 replicates each, with the three dominance coefficients represented by triangles, squares, and crosses, respectively. Other parameters used for these examples were $s = -0.0002$, $m = 0.1$, 100 demes of 100 diploid individuals each, and colonization by four individuals with a probability of common origin equal to 1/2. The probability of fixation is increased substantially by the reduction in N_e that accompanies extinction dynamics. (B) The parameters in these examples were $h = 0.01$, $s = -0.0002$ with 100 demes of 100 diploid individuals. Points represent the results of 10^8 simulations.

Local Genetic Load and the Consequences of Migration

In subdivided populations, weakly deleterious alleles can rise by drift to high frequencies within local populations, even if selection is effective at keeping their overall frequency low throughout the species. Crow (1948) proposed that this could be the mechanism for the commonly observed pattern of heterosis, the increase in fitness often observed in hybrids between different populations. We examined this hypothesis using Wright's distribution of allele frequencies for the island model (Whitlock et al., 2000; Ives and Whitlock, 2002) and found that Crow's hypothesis was extremely credible. We referred to the reduction in mean fitness caused by this local increase in the frequency of deleterious alleles *local drift load* and showed that reasonably large values of heterosis were consistent with what is known about mutation rates and population structure. These results have been extended by Morgan (2002) and Glémin (2003). Morgan (2002) showed that

$$\frac{\overline{w}_{hybrid}}{\overline{w}_{local}} = \left(\frac{(1-hs)^2}{1-s}\right)^{nV_{among}} \tag{7.14}$$

where V_{among} is the variance among demes in allele frequency as defined and n is the number of loci. With this we can write a prediction for the heterosis in terms of F_{ST} and $\overline{q}$:

$$heterosis = \frac{\overline{w}_{hybrid}}{\overline{w}_{local}} - 1 = \left(\frac{(1-hs)^2}{1-s}\right)^{nF_{ST}\overline{q}\overline{p}} - 1 \tag{7.15}$$

If the metapopulation itself is relatively large and at equilibrium, then $\overline{p} \cong 1$ and $\overline{q}$ is approximately $\hat{\overline{q}}$ from Eq. (7.7).

Heterosis has an interesting biological consequence. If offspring formed by crosses between demes have selective advantage, then the offspring of migrants will have increased fitness (Ingvarsson and Whitlock, 2000; Morgan, 2002). Thus the genetic effects of migration will be increased relative to the actual observed migration rate. The *effective migration rate* for a neutral locus is approximately

$$m_e = m\, e^{heterosis/\tilde{r}}, \tag{7.16}$$

where $\tilde{r}$ is the harmonic mean recombination rate between the neutral locus and all selected loci (Ingvarsson and Whitlock, 2000). For low values of F_{ST}, the magnification of the effective rate of migration can be severalfold. This can be counterbalanced or reversed by sufficient local adaptation or strong differences among populations in epistatic interactions.

Load in Subdivided Populations, a Summary

Several types of load are affected by population structure. Mutation load tends to decline at equilibrium with structure, and migration load is lowered with lower migration rates, whereas drift load, segregation load, and local drift load tend to increase. Because these different genetic loads are cumulative, the mean fitness of the population with three different types of genetic load is approximately $(1 - L_1)(1 - L_2)(1 - L_3)$. If the loads are small (they are not in general expected to be) then the overall load is approximated by the sum over the types of load. Whether population structure increases or decreases mean fitness on average depends on a large number of circumstances. If habitat conditions vary strongly, then population structure allows local adaptation (in other words, reducing migration load) and this effect can be paramount. However, if migration rates become too small and local population size is low, then local drift load will become very important and essentially the population will suffer from inbreeding depression. Species-level drift load could become important if there is a lot of variance among demes in reproductive success and if the total census size of the species was small (so that the effective size was low), but is likely not very important if the effective size of the species is over about 10,000. Mutation load may be reduced by population structure (at equilibrium), but not by more than a half. In some species, for example, those in which the genomic deleterious mutation rate is high, this could be a major effect; but for species with lower mutation rates, this could be a trivial effect. The balance of the effects of these processes will depend on the specifics of the species.

7.6 CONCLUSIONS AND INCONCLUSIONS

The course of evolution is changed quantitatively and qualitatively by the subdivision of populations over space. All of the population genetic processes that act in unstructured populations are affected, sometimes substantially, and some kinds of evolution are only possible with structured populations. This chapter focused on the former: quantitative changes in evolutionary rates from population subdivision. Even with uniform selection, the rate of genetic drift and the response to selection are changed substantially.

For some of the quantities described in this chapter (e.g., N_e, the probability of fixation of beneficial alleles), results have already been found for a special case of population structure: the island model. The island model is the oldest in population genetics, and it is rightfully the first to turn to when considering new problems because of its simplicity. Unfortunately, the very simplicity that make it appealing also makes it an aberration. The island model assumes that all demes are equal; not only do all demes have the same population size and migration and immigration rates, but more importantly, it implicitly assumes that all demes contribute exactly equally to the next generation. Clearly these conditions do not apply to most (or even all) natural populations, but this would not matter if these assumptions had no effect on our evolutionary predictions. Unfortunately, this assumption of equal reproductive success has a qualitative effect on our predictions, especially for questions that involve effective size. In this subtle but key respect, the island model is an extreme model, and some of the predictions made from the island model are extreme as a result.

Fortunately, it is possible to derive theory that predicts the necessary parameters for other models of population structure. The last couple of decades have seen a lot of development of models, including isolation by distance, local extinction, population size change, variable migration rates, and asymmetric migration. Even more fortunately, the results described in this chapter show that, at least for weak selection, most of the effects of population structure can be described in a few summary statistics, especially F_{ST} and N_e. This is extremely useful because we know a lot about how F_{ST} is changed by various demographic processes and we have the theory to predict the effective size for a broad class of models. F_{ST} in particular has been very well studied, with many empirical studies devoted to measuring it in a wide variety of species and a large number of theoretical models. These include extinction and recolonization (Wade and McCauley, 1988; Whitlock and McCauley, 1990), population fission and fusion (Whitlock, 1994), source–sink models (Gaggiotti, 1996), and stepping-stone models (Kimura and Weiss, 1964). In all of these cases, F_{ST} differs significantly from that predicted by the island model, and in most the effective population size is also substantially different (and usually much less than the census size). Moreover, it is usually straightforward to calculate F_{ST} even for a novel system.

As an aside, the reason that F_{ST} has been measured empirically so often has little to do with its importance to predict the effects of population structure on selection or drift. F_{ST} has been measured usually because of the false hope that it could be used to estimate the number of migrants coming into a population per generation (Whitlock and McCauley, 1999). It is fortunate then that this effort has not been wasted, and it is important not to throw the evolutionary baby out with the estimator bathwater. F_{ST} is an excellent descriptor of the nature of population structure and should be calculated in genetic studies of metapopulations. Unfortunately, the same cannot be said for its properties as an estimator of dispersal.

There are many unresolved questions on evolution on space. We have made some progress in understanding the effects of population structure on response to uniform selection, but we have not yet made similar progress with the heterogeneous selection case. All of the results considered here deal with discrete populations in which organisms are grouped into demes with the space between them empty. Most of the questions presented here have not solved for the spatial case in which individuals are spread continuously over space, a much more challenging topic. These results all assume weak selection, yet some of the most interesting cases involve selection coefficients stronger than migration rates.

We also need many more empirical studies on these topics. This chapter has not reviewed the empirical literature at all, but most of the theory presented here remains untested experimentally. Furthermore, we need better measures of some key parameters. The dominance coefficient has a tendency to cancel out of panmictic calculations, but this is not true for evolution in structured populations; we have very few estimates of the distribution of dominance coefficients. We desperately need more empirical studies of the effective size of structured populations. We also need to develop individual-weighted estimators of F_{ST}, as has been shown to be required by this theory.

The subdivision of a species over space can affect its evolution strongly and in a variety of ways. Because most species in nature are subdivided over space, it behooves us to understand this nearly ubiquitous feature of the natural world.

U.S. FISH AND WILDLIFE SERVICE
5-YEAR REVIEW for
BLACK-FOOTED FERRET
(*Mustela nigripes*)

Species Reviewed: Black-footed ferret (*Mustela nigripes*)

Federal Register Notice of Listing Determination:

- March 11, 1967. Endangered Species Preservation Act of 1966; Endangered Status for the Black-footed ferret (32 FR 4001).
- June 2, 1970. Endangered Species Conservation Act of 1969; Revised Listing of the Black-footed ferret as Endangered (35 FR 8491).
- January 4, 1974. Endangered Species Act of 1973; Listing as Endangered (39 FR 1171).

Federal Register Notice Announcing Initiation of this Review: August 10, 2018. Endangered and Threatened Wildlife and Plants; 5-Year Status Reviews of 11 Species in the Mountain-Prairie Region (83 FR 39771).

Lead Region: Department of Interior Region 7, Black-footed Ferret Recovery Program, Pete Gober, Recovery Coordinator, (720) 626-5260.

Classification: Endangered

Methodology used to complete the review: In accordance with section 4(c)(2) of the Endangered Species Act of 1973, as amended (Act), the purpose of a 5-year review is to assess each threatened species and endangered species to determine whether its status has changed and if it should be classified differently or removed from the Lists of Threatened and Endangered Wildlife and Plants. The U.S. Fish and Wildlife Service (Service) recently evaluated the biological status of the black-footed ferret as part of a Species Status Assessment (SSA) to inform this 5-year review and recovery planning and implementation for the species. Our SSA report (Service 2019) for the black-footed ferret included input from tribes, state wildlife agencies, Federal land management agencies, and non-governmental organizations (NGOs) engaged in black-footed ferret conservation efforts throughout its range, and was independently reviewed by peer reviewers and partners. The SSA report represents our evaluation of the best available scientific information, including the resource needs and the current and future condition of the species. We developed five future scenarios with respect to land and species management conditions, which we analyzed under two future climate predictions, to portray a range of possible future conditions for the species. The SSA report is the scientific basis for this 5-year review decision-making process.

Additionally, we solicited data for this review from interested parties through an August 10, 2018, Federal Register Notice announcing this review (83 FR 39771). Information we received from this data call included summaries of recent conservation actions by non-governmental organizations (NGOs).

REVIEW ANALYSIS

Updated Information and Current Species Status

Biology and Habitat:

Our SSA report (Service 2019) provides a detailed summary of the biology, habitats, and current and future condition for the black-footed ferret, which we summarize below. The black-footed ferret is the only ferret species native to North America, and its historic distribution overlapped with the distributions of three prairie dog species: the black-tailed prairie dog (*Cynomys ludovicianus*), Gunnison's prairie dog (*C. gunnisonii*), and the white-tailed prairie dog (*C. leucurus*). It is an obligate associate of these three prairie dog species, and depends almost exclusively on prairie dogs for food and on prairie dog burrows for shelter (Hillman 1968, Biggins at al. 2006a). The species was common historically; however, its secretive habits (nocturnal and often underground) probably made it difficult to observe (Forrest et al. 1985, Anderson et al. 1986, Clark 1989). Anderson et al. (1986) stated that prairie dog habitat 100 years ago may have supported 500,000-1,000,000 black-footed ferrets given a conservative estimate of 41,000,000 hectares (ha) of prairie dog colonies and one ferret per 40-60 ha (Forrest et al. 1985). At present, the species has been reintroduced to a small portion of its historic range, with 29 discrete reintroduction sites being established since recovery efforts began in 1991. As of December 9, 2019, 13 of 29 reintroduction sites are active, with an estimated wild population of approximately 325 individuals. The captive population is divided between six captive breeding facilities, and numbers 301 individuals.

To assess the current status, future status, and overall viability of the black-footed ferret, we used the conservation biology principles of resiliency, redundancy, and representation. Specifically, we considered the ecological requirements of the black-footed ferret at the individual, population, and species levels, and described the stressors influencing the viability of the species.

At the individual level, the primary requirement for all black-footed ferret life stages is prairie dogs. At the population level, black-footed ferret populations need at least 30 breeding adults, which requires at least 1,200-1,800 ha of black-tailed prairie dog habitat or 2,500-4,000 ha of Gunnison's or white-tailed prairie dog habitat, depending on prairie dog density (Service 2013). Populations also need some level of connectivity, a sufficient rate of juvenile survival, and larger, contiguous prairie dog colonies to maintain resiliency to stochastic events. At the species level, the black-footed ferret needs multiple (≥20), resilient populations that display a breadth of ecological and genetic diversity across its historic range, including black-tailed, Gunnison's, and white-tailed prairie dog habitats. A captive breeding population is also needed to provide individuals for release at reintroduction sites, thereby increasing resiliency of those populations, and to provide additional redundancy in the case of catastrophic events that could affect reintroduction sites, as well as to maintain the theoretical genetic diversity that is needed for the species to adapt to changing conditions.

The SSA report summarizes the current and projected future conditions of the black-footed ferret to assess the overall viability of the species now and into the future. For the purposes of the SSA, we defined viability as the ability of the black-footed ferret to sustain populations in the wild into the future. Additionally, since the continued persistence of the black-footed ferret depends heavily on the ability to release captive-reared individuals into the wild in order to establish new reintroduction sites and maintain existing reintroduction sites throughout its potential range, we also evaluated the viability of the captive population to provide individuals for these purposes into the future.

For our analyses, we divided the wild (i.e., reintroduced) black-footed ferret population into 29 analysis units that correspond to locations where the species has been purposely reintroduced. The captive population was divided into six analysis units that correspond to the captive breeding facilities currently participating in the black-footed ferret recovery program. For the wild population, we evaluated the resiliency of each analysis unit using the metrics of five-year mean number of breeding adults, the five-year average ferret family rating (an index of habitat suitability encompassing area and prairie dog density; see Biggins et al. 1993 and Biggins et al. 2006b), annual plague management level, annual ferret vaccination level, ferret population persistence, and level of prairie dog population conservation. These metrics either directly or indirectly addressed four primary stressors of concern: sylvatic plague, drought, prairie dog poisoning and shooting, and declining genetic fitness, with declining genetic fitness defined as increased inbreeding and declining genetic diversity. For the captive population, we evaluated the resiliency of each analysis unit using the metrics of percent whelping success, mean number of kits born per litter, and percentage of kits weaned to assess breeding success, animal condition, animal husbandry effectiveness, and declining genetic fitness.

Using the metrics referenced above, we determined that two reintroduction sites were in high condition (high resiliency), eight were in moderate condition (moderate resiliency), four were in low condition (low resiliency), and 15 were extirpated. For the captive population, we determined that one facility was in high condition, four were in moderate condition, and one was in low condition. We note that considerable management inputs (primarily plague management and population augmentation with captive-reared animals for the wild population and managed breeding for the captive population) are required to maintain the of resiliency of each population, and most if not all of the reintroduction sites that are extirpated became so due to the effects of sylvatic plague. Currently, the wild black-footed ferret population is found within all of the ecological settings it occupied historically (black-tailed, Gunnison's, and white-tailed prairie dog habitat), although its representation within Gunnison's prairie dog habitat is limited to only one site. Representation in a genetic context is inherently limited due to the small founder population of seven animals (Hutchins et al. 1996, Wisely 2006), and the current genetic diversity in the captive population is estimated to be 85.66 percent of the founder population (Graves et al. 2018). Although the effects of declining genetic diversity on the reintroduced black-footed ferret population are not known, sperm structural abnormalities in captive black-footed ferret males associated with inbreeding may be responsible for declining reproductive success in the captive black-footed ferret population (Santymire et al. 2019).

We projected the future viability of the black-footed ferret by forecasting the conditions of our metrics for each analysis unit under five potential future scenarios, as described further in the SSA Report (Service 2019). Our future scenarios varied based on four main stressors: sylvatic plague, drought, prairie dog poisoning and shooting, and declining genetic fitness; as well as levels of conservation efforts. We forecasted each scenario to two time periods, approximately 10 and 20 years into the future, and under two climate scenarios that varied with respect to evaporative deficit. The projected future condition of each population varied by scenario, but we predicted that both populations would decline in viability under every scenario except for scenarios where conservation efforts increased relative to current levels. Overall, we project that the effects of sylvatic plague, declining genetic fitness, and the lack of suitable habitat will continue to limit the viability of the black-footed ferret, and management inputs will continue to be required in order to maintain current levels of viability. Moreover, management inputs will need to be expanded and improved in effectiveness in order to increase viability for the species.

Threats Analysis (threats, conservation measures, and regulatory mechanisms):
In our SSA report, we evaluated a number of stressors that may affect the resiliency of black-footed populations, including sylvatic plague, declining genetic fitness, drought, agricultural land conversion, poisoning of prairie dogs, recreational shooting of prairie dogs, range management practices, urbanization, and energy development (Service 2019, pp. 13-42). Based on our evaluation of these stressors, only four (sylvatic plague, declining genetic fitness, drought, and the combined category of recreational shooting of prairie dogs and prairie dog poisoning) were carried forward in our current and future analyses, which included projections under two different greenhouse gas emission scenarios (Service 2019, pp. 56-57) Additional current and potential future rangewide threats to the black-footed ferret identified in the most recent recovery plan (Service 2013) and 5-year review (79 FR 25883) included lack of prairie dog management sufficient for ferrets. A summary of the stressors analyzed in the SSA report and their relationship with the five categories of threats specified in section 4(a)(1) of the Act is found in Table 1.

Table 1. Summary of threats affecting the black-footed ferret and the associated listing factors.

Listing Factor	Threat Description
Factor A: The present or threatened destruction, modification, or curtailment of its habitat or range	Analyzed as a threat that occurred in the past in the SSA report, but not identified as a current threat in the SSA report or in previous analyses.
Factor B: Overutilization for commercial, recreational, scientific, or educational purposes	Synergistic effects of recreational shooting and sylvatic plague (see Factor C, below) identified as an imminent threat of low magnitude for black-footed ferret populations located in black-tailed prairie dog habitat.

Factor C: Disease or predation	Sylvatic plague (both direct impact to black-footed ferrets and indirect impact of modification of habitat through the loss of prairie dog habitat) identified as an imminent threat of high magnitude. Effects of sylvatic plague are exacerbated by other sources of prairie dog mortality (see Factors B and E).
Factor D: Inadequacy of existing regulatory mechanisms	Lack of purposeful management of prairie dog populations to provide sufficient habitat for black-footed ferrets identified as an imminent threat of high magnitude (Service 2013); SSA report notes the need for ongoing management of prairie dog populations to maintain and increase black-footed ferret resiliency, redundancy, and representation.
Factor E: Other natural or manmade factors	Poisoning of prairie dogs at black-footed ferret reintroduction sites constitutes a high magnitude, imminent threat, especially in conjunction with sylvatic plague (see Factor C). Climate change constitutes an imminent threat of moderate magnitude by increasing the frequency and severity of droughts, which reduces black-footed ferret habitat suitability. Declining genetic fitness represents an imminent threat of moderate magnitude due to observed effects on captive population performance.

RECOMMENDATION ON SPECIES STATUS

The Act defines an endangered species as any species that is "in danger of extinction throughout all or a significant portion of its range" and a threatened species as any species that is "likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." After evaluating threats to the species and assessing the cumulative effects of the threats under the section 4(a)(1) factors, we conclude that the black-footed ferret is in danger of extinction throughout all of its range. The range of this formerly widespread species has been severely reduced, currently existing in the wild at only 13 reintroduction sites, and the species still faces threats, such as sylvatic plague, that are largely unabated and have significant and direct impacts to population resiliency. Currently, significant management inputs (primarily sylvatic plague mitigation and the maintenance of a captive breeding program) are required to maintain black-footed ferret populations in the wild, and cessation of these efforts would likely result in the extinction of the species. Specifically, low population numbers in the reintroduced population, declining reproductive performance in the captive population, continued risk of reintroduction site extirpations due to the impacts of sylvatic plague, and lack of suitable habitat collectively result in low population resiliency for many analysis units, and reduces redundancy and representation for the species as a whole, such that the viability of the species continues to be at risk. These factors support our previous evaluation that the black-footed ferret continues to meet the definition of an endangered species under the Act. Therefore, our review of new information, as documented in our SSA report (Service 2019) and summarized in this 5-year review, does not change our evaluation of species status and the threats affecting the species under the factors in section 4(a)(1) of the Act from our last and most recent review of the species (May 6, 2014; 79 FR 25883). Therefore, we recommend no change in status to the species at this time.

U.S. FISH AND WILDLIFE SERVICE
5-YEAR REVIEW
BLACK-FOOTED FERRET (*Mustela nigripes*)

CURRENT CLASSIFICATION: Endangered

RECOMMENDATION RESULTING FROM THE 5-YEAR REVIEW:

____ Downlist to Threatened
____ Uplist to Endangered
____ Delist:
    ____ Extinction
        ____ Recovery
        ____ Original data for classification in error
_X_ No change is needed

APPROPRIATE LISTING/RECLASSIFICATION PRIORITY NUMBER, IF APPLICABLE: No change from 2C.

RECOMMENDATIONS FOR FUTURE ACTIONS:

- Update Species Status Assessment report with Population Viability Analysis (PVA), and other new information as needed
- Develop revised Recovery Plan based on Species Status Assessment and Black-footed Ferret Recovery Program review (timeframe to be determined)

FIELD OFFICE APPROVAL:

Approve: P Gob ______________________ Date: 1/21/20
Pete Gober
U.S. Fish and Wildlife Service
Black-footed Ferret Recovery Coordinator

The lead Field Office must ensure that other offices within the range of the species have been provided adequate opportunity to review and comment prior to the review's completion. The lead field office should document this coordination in the agency record.

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Species Status Assessment Report for the Black-footed Ferret (*Mustela nigripes*)

Photo credit: John Ashley

Version 1.0
December 12, 2019

Prepared by the U.S. Fish and Wildlife Service Black-footed Ferret Recovery Program and members of the Black-footed Ferret Recovery Implementation Team

Acknowledgements

We would like to thank the following individuals for providing substantial information and insights for this SSA report: Tyler Abbott (U.S. Fish and Wildlife Service), Nichole Bjornlie (Wyoming Game and Fish Department), Kristy Bly (World Wildlife Fund), Robyn Bortner (U.S. Fish and Wildlife Service), David Eads (U.S. Geological Survey), Steve Forrest (Defenders of Wildlife), Shaun Grassel (Lower Brule Sioux Tribe), Lauri Hanauska-Brown (Montana Fish, Wildlife, and Parks), Holly Hicks (Arizona Game & Fish Department), Tina Jackson (Colorado Parks and Wildlife), Chris Keefe (Bureau of Land Management), Silka Kempema (South Dakota Game, Fish, and Parks), Travis Livieri (Prairie Wildlife Research), David Lucas (U.S. Fish and Wildlife Service), Randy Matchett (U.S. Fish and Wildlife Service), Brian Maxfield (Utah Division of Wildlife Resources), Matt Peek (Kansas Department of Wildlife, Parks, and Tourism), Rachel Santymire (Lincoln Park Zoo), Greg Schroeder (National Park Service), Dan Tripp (Colorado Parks and Wildlife), and Rachel Williams (U.S. Fish and Wildlife Service). We thank Sarah Backsen, Julie Reeves, and Justin Shoemaker of the U.S. Fish and Wildlife Service with their assistance in conducting an expert workshop to solicit stakeholder perspectives. We would also like to thank everyone who reviewed initial drafts of the report and provided helpful comments, as well as the two peer reviewers.

Executive Summary

This report summarizes the results of a Species Status Assessment (SSA) that the U.S. Fish and Wildlife Service (Service) has completed for the black-footed ferret (*Mustela nigripes*). The black-footed ferret is the only ferret species native to North America, and its historic distribution overlapped with the distributions of three prairie dog species: the black-tailed prairie dog (*Cynomys ludovicianus*), Gunnison's prairie dog (*C. gunnisonii*), and the white-tailed prairie dog (*C. leucurus*). This SSA report summarizes the current and projected future conditions of the black-footed ferret to assess the overall viability of the species now and into the future. For the purposes of this SSA, we define viability as the ability of the black-footed ferret to sustain populations in the wild into the future. Additionally, since the continued persistence of the black-footed ferret depends heavily on the ability to release captive-reared individuals into the wild in order to establish new reintroduction sites and maintain existing reintroduction sites throughout its potential range, we also evaluate the viability of the captive population to provide individuals for these purposes into the future.

To assess the current status, future status, and overall viability of the black-footed ferret, we used the conservation biology principles of resiliency, redundancy, and representation (collectively, the 3Rs). Specifically, we identified the ecological requirements of the black-footed ferret at the individual, population, and species levels, and described the stressors influencing the viability of the species. The black-footed ferret needs multiple, resilient populations distributed across its range in a variety of ecological settings to persist into the future and to avoid extinction. For our analyses, we divided the wild (i.e., reintroduced) black-footed ferret population into 29 analysis units that correspond to locations where the species has been purposely reintroduced. The captive population was divided into six analysis units that correspond to the captive breeding facilities currently participating in the black-footed ferret recovery program. For the wild population, we evaluated the resiliency of each analysis unit using the metrics of five-year mean number of breeding adults, the five-year average ferret family rating (an index of habitat suitability encompassing area and prairie dog density), annual plague management level, annual ferret vaccination level, ferret population persistence, and level of prairie dog population protection. These metrics either directly or indirectly addressed four primary stressors of concern: sylvatic plague, drought, prairie dog poisoning and shooting, and declining genetic fitness, with declining genetic fitness defined as increased inbreeding and declining genetic diversity. For the captive population, we evaluated the resiliency of each analysis unit using the metrics of percent whelping success, mean number of kits born per litter, and percentage of kits weaned to assess breeding success, animal condition, animal husbandry effectiveness, and declining genetic fitness.

The historical condition of the black-footed ferret is difficult to quantify due to a lack of reliable historical data and the secretive nature of the species. At present, the species has been reintroduced to a small portion of its historic range, with 29 discrete reintroduction sites being established since recovery efforts began in 1991. As of 2019, 14 of 29 reintroduction sites are active, with an estimated wild population of approximately 340 individuals. The captive

population is divided between six captive breeding facilities, and numbers 301 individuals. Using the metrics referenced above, we determined that two reintroduction sites were in high condition (high resiliency), eight were in moderate condition (moderate resiliency), four were in low condition (low resiliency), and 15 were extirpated. For the captive population, we determined that one facility was in high condition, four were in moderate condition, and one was in low condition. We should note that considerable management inputs (primarily plague management and population augmentation with captive-reared animals for the wild population and managed breeding for the captive population) are required to maintain the of resiliency of each population, and most if not all of the reintroduction sites that are extirpated became so due to the effects of sylvatic plague. Currently, the wild black-footed ferret population is found within all of the ecological settings it occupied historically (black-tailed, Gunnison's, and white-tailed prairie dog habitat), although its representation within Gunnison's prairie dog habitat is limited to only one site.

We predicted the future viability of the black-footed ferret by forecasting the conditions of our metrics for each analysis unit under five potential future scenarios. Our future scenarios varied based on four main stressors, sylvatic plague, drought, prairie dog poisoning and shooting, and declining genetic fitness, as well as levels of conservation efforts. We forecasted each scenario to two time periods, approximately 10 and 20 years into the future. The projected future condition of each population varied by scenario, but we predicted that both populations would decline in viability under every scenario except for scenarios where conservation efforts increased relative to current levels. Overall, we predict that the effects of sylvatic plague and the lack of suitable habitat will continue to limit the viability of the black-footed ferret, and management inputs will continue to be required in order to maintain current levels of viability. Moreover, management inputs will need to be expanded and improved in effectiveness in order to increase viability for the species. We acknowledge that our assessment of future conditions is a projection involving uncertainty. However, our future scenarios are designed to capture the full range of future conditions that could plausibly occur, and we used the best available science for our analyses and acknowledged any key assumptions and uncertainties throughout this SSA report.

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Chapter 1. Introduction

This report summarizes the results of a Species Status Assessment (SSA) conducted by the U.S. Fish and Wildlife Service (Service) for the black-footed ferret (*Mustela nigripes*). The black-footed ferret is a medium-sized carnivore historically found in the Great Plains and Intermountain West states of Arizona, Colorado, Kansas, Montana, Nebraska, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, Utah, and Wyoming, as well as the Canadian province of Saskatchewan and the Mexican state of Chihuahua. The species was thought to be extinct in 1979, until it was rediscovered in 1981 in Meeteetse, Wyoming. A captive breeding program was established using individuals from this population, and all extant ferrets are descendants of this captive population. At present, the black-footed ferret is found only in a reintroduced population at multiple sites in the states of Arizona, Colorado, Kansas, Montana, New Mexico, South Dakota, Utah, and Wyoming, and a captive population housed at facilities located in Arizona, Colorado, Kentucky, Virginia, and Ontario, Canada.

We used the SSA framework (Smith et al. 2018) to develop a comprehensive analysis of the black-footed ferret's biology, the stressors affecting its status, its current biological status, and to project the future status of the species under various future scenarios. This SSA report summarizes the results of our analysis, and provides a means of assessing the viability of the black-footed ferret. As new information becomes available, we intend to revise this SSA as needed so it can serve as a foundational document for all functions of the Service's Ecological Service program, such as consultation and recovery planning.

The purpose of this SSA report is to provide a scientific foundation for the Service's 5-year status review of the listing status of the black-footed ferret under the Endangered Species Act of 1973, as amended (Act) (16 U.S.C. 1531 *et seq.*). Importantly, this SSA report is not a decision document, but instead provides the scientific information needed to support future decisions made by the Service under the Act. The 5-year review finding will be made by the Service after reviewing this SSA report and all relevant laws, regulations, policies, and conservation efforts, and the Service will announce its finding independently.

1.1 Listing History and Previous Federal Actions

The black-footed ferret was listed as an endangered species in 1967 (32 FR 4001, March 11, 1967) and again in 1970 (35 FR 8491, June 2, 1970) under early endangered species legislation and was "grandfathered" as an endangered species under the Act in 1973. Black-footed ferrets are exempt from the requirement to designate critical habitat because they were listed prior to the 1978 amendments to the Act requiring critical habitat. The first recovery plan for the black-footed ferret was published in 1978 (Linder et al. 1978), and was revised in 1988 (USFWS 1988) and again in 2013 (USFWS 2013a). A 5-year review was issued concurrently with the 2013 recovery plan revision, and retained the endangered status for the species.

1.2 The Species Status Assessment (SSA) Framework

This SSA report summarizes the results of our in-depth review of the black-footed ferret's biology and stressors, an evaluation of its biological status, and an assessment of the resources and conditions needed to maintain long-term viability. For the purposes of this assessment, we define viability as the ability of the species to sustain populations in the wild into the future in a biologically meaningful timeframe, which is 10-20 years for our analysis. We chose this relatively short timeframe due to the high population turnover rates of the black-footed ferret and its primary prey, prairie dogs, the sudden and chronic effects of sylvatic plague, and the small population sizes at many reintroduction sites that are vulnerable to short-term stochastic effects. Since the viability of this species in the wild is also dependent on the presence of a captive population, we also assess the ability of the species to sustain a captive population over the same timeframe.

Using the SSA Framework (Figure 1), we evaluated what the black-footed ferret needs to be viable into the future by characterizing the current and future statuses of the species using the concepts of resiliency, redundancy, and representation (the "3Rs") from conservation biology (Shaffer and Stein 2000, Smith et al. 2018).

Resiliency is the ability of populations to tolerate natural, annual variation in their environment and to recover from periodic or random disturbances, known as stochastic events. Resiliency can be measured using metrics like vital rates, such as annual births and deaths, and population size. In general, populations with high abundance and stable or increasing population trends are more resilient than those with limited resources or declining populations. Populations with high resiliency can better withstand stochastic changes in demography or their environment due to natural or anthropogenic disturbances.

Redundancy is the ability of a species to withstand catastrophic events, such as a rare, destructive natural event that affects multiple populations. Redundancy is measured by the duplication and distribution of populations across the range of the species. The more redundant a species, or the greater number of populations a species has distributed over a larger landscape, the better able it is to recover from catastrophic events. Redundancy helps "spread the risk" and ensures that not all populations are extirpated at once due to a catastrophic event.

Representation is the ability of a species to adapt to changing physical (climate, habitat) and biological (diseases, predators) conditions. Representation can be measured by looking at the genetic, morphological, behavioral, and ecological diversity within and between populations across a species' range. The more representation, or diversity, a species has, the more likely it is to be able to adapt and persist with natural or human-caused changes to its environment.

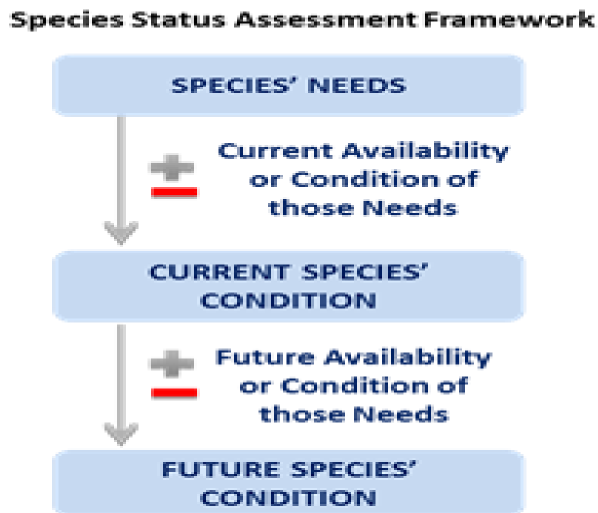

Figure 1. The three phases of the SSA Framework used to guide this analysis. To assess the viability of the black-footed ferret, we evaluated the species' needs, the current availability and condition of those needs, and the current condition of the species. We then predicted the future condition of the species based on the projected future availability and condition of the identified needs of the species.

For the purpose of this SSA, viability is defined as the ability of the species to sustain populations in the wild into the future in a biologically meaningful timeframe. Viability is not a single state; rather, there are degrees of viability. In other words, a Species Status Assessment does not determine if a species is or is not viable. Instead, we characterize the resiliency, redundancy, and representation a species currently exhibits and predict how these characteristics may change in the future. Generally speaking, species with higher resiliency, redundancy, and representation are more protected from environmental changes, can better tolerate stressors and adapt to changing conditions, and are thus more viable than species with low levels of the 3Rs.

To assess the viability of the black-footed ferret, we analyzed its ecology, historic and current conditions, and projected the viability of the species under a number of future scenarios, all in the context of the 3Rs and using the best scientific data available. Chapter 2 of this SSA report summarizes the biology, ecology, and needs of the black-footed ferret at the individual, population, and species levels. Chapter 3 examines the stressors and conservation measures that affect the resiliency of wild and captive black-footed ferret populations and analyzes the historical and current conditions of the species. Chapter 4 projects the future condition of the species under five scenarios. In Chapter 5, we summarize all of the information presented in this SSA and analyze the overall viability of the black-footed ferret.

1.3 Summary of Recent Information

Since the 2013 publication of the revised Black-footed Ferret Recovery Plan (USFWS 2013a), we have evaluated new peer-reviewed literature and solicited new information from partner agencies and organizations throughout the historic range of the black-footed ferret, including, but not limited to, state wildlife management agencies, tribes, non-governmental conservation organizations, the U.S. Forest Service, Bureau of Land Management, and National Park Service. These organizations are members of the Black-footed Ferret Recovery Implementation Team (BFFRIT), which serves as an expert source of up-to-date demographic and distribution data for the species. Specifically, we requested information on the following topics:

- The species' distribution, population levels, and population trends in the wild (i.e. at reintroduction sites);
- The species' population levels and trends in captive settings;
- The magnitude and severity of sylvatic plague and other diseases at various reintroduction sites;
- Other potential threats to the species, including, but not limited to, inbreeding depression, energy development, agricultural conversion, recreational shooting of prairie dogs (*Cynomys spp*.), and poisoning;
- Updates to laws, regulations, policies, or management plans that may apply to the species; and
- Any ongoing conservation actions for the species and its habitats.

Our literature review and data solicitation found that there was new information for wild populations on sylvatic plague dynamics and management, development of additional black-footed ferret reintroduction sites through the Black-footed Ferret Programmatic Safe Harbor Agreement (USFWS 2013b), and conservation efforts undertaken by individual states and tribes through the use of state-or tribe-specific black-footed ferret management plans. New information obtained for the captive population included information on the production of kits from captive breeding partners under the auspices of the Black-footed Ferret Species Survival Plan® (SSP®). New information was also obtained for the emerging role of genomics in the potential management both the captive and reintroduced populations. In addition, several pertinent peer-reviewed papers have been published since 2013 investigating the application and efficacy of the insecticide deltamethrin, the systemic pulicide fipronil, and oral Sylvatic Plague Vaccine (SPV) to manage the non-native bacterium *Yersinia pestis* that causes deadly epizootics of sylvatic plague, as well as potential application of genomics to aid both captive and wild populations.

We incorporated these data, which include spatial data, peer-reviewed literature, reports, and personal communications with experts, into various parts of the SSA, including the analysis of the current population levels and distribution of the black-footed ferret and the severity of stressors and related conservation actions. If we lacked specific data for some aspect of our analysis, we used information obtained through communication with experts at various meetings of BFFRIT subcommittees, including the Conservation Subcommittee, Related Species Subcommittee, Disease Subcommittee, and Managed Care Subcommittee.

Chapter 2. Species Ecology and Needs

In this chapter, we provide basic biological information about the black-footed ferret, including its taxonomic history and relationships, morphological description, physical environment, and reproductive and other life history traits. We then describe the needs of the black-footed ferret at the individual, population, and species levels. This chapter is not an exhaustive review of the species' natural history, but rather provides the biological basis for the SSA analyses in this report.

2.1 Life History

2.1.1 Taxonomy and Description

The black-footed ferret is in the Order Carnivora, Family Mustelidae, Genus *Mustela*, and Subgenus *Putorius*. No subspecies are recognized (Hillman and Clark 1980, Anderson et al. 1986). The species is one of four members of the genus *Mustela* in North America that also includes the ermine (*M. erminea*), long-tailed weasel (*M. frenata*), and least weasel (*M. nivalis*) (Wilson and Ruff 1999, Kurose et al. 2008). The black-footed ferret is the only ferret species native to the Americas. Other ferret species in the subgenus are the Siberian polecat (*M. eversmanii*) and the European ferret (*M. putorius*) (Hillman and Clark 1980, Anderson et al. 1986), which has been domesticated and sold as a pet. The black-footed ferret is most closely related to the Siberian polecat (Hillman and Clark 1980, Anderson et al. 1986). The earliest fossil record of the black-footed ferret is from approximately 100,000 years ago and the species was first formally described in 1851 by J.J. Audubon and J. Bachman (Anderson et al. 1986, Clark 1986).

The black-footed ferret is a medium-sized mustelid, typically weighing 645–1125 grams (1.4-2.5 pounds) and measuring 479–600 millimeters (19-24 inches) in total length. Upper body parts are yellowish buff, occasionally whitish; feet and tail tip are black; and a distinctive black "mask" occurs across the eyes (Hillman and Clark 1980, Anderson et al. 1986)

2.12 Habitat and Distribution

The black-footed ferret was historically found throughout the Great Plains, mountain basins, and semi-arid grasslands of North America, and its distribution coincided with the ranges of the black-tailed prairie dog (*Cynomys ludovicianus*), Gunnison's prairie dog (*C. gunnisonii*), and white-tailed prairie dog (*C. leucurus*) (Hillman and Clark 1980, Figure 2). There has been no documented occurrence of the ferret within the range of either the Utah prairie dog (*C. parvidens*) or the Mexican prairie dog (*C. mexicanus*), whose ranges are small and disjunct from other prairie dog species (Lockhart et al. 2006). The species was common historically; however, its secretive habits (nocturnal and often underground) probably made it difficult to observe (Forrest et al. 1985, Anderson et al. 1986, Clark 1989). Anderson et al. (1986) stated that prairie dog habitat 100 years ago may have supported 500,000-1,000,000 black-footed ferrets given a conservative estimate of 41,000,000 hectares (ha) of prairie dog colonies and one ferret per 40-60 ha (Forrest et al. 1985).

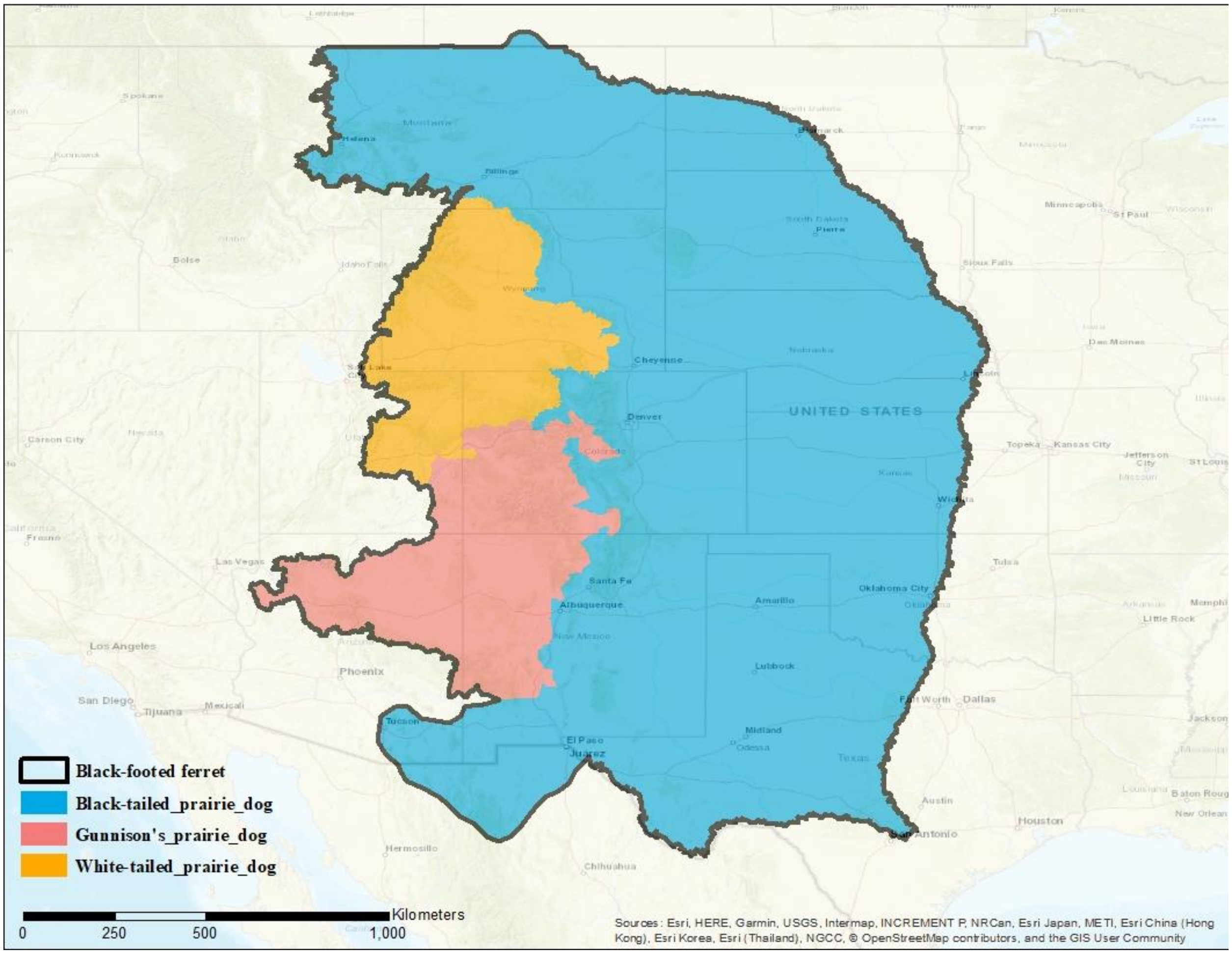

Figure 2. Historical distribution of the black-footed ferret and the distribution of black-tailed, Gunnison's, and white-tailed prairie dogs.

2.1.3 Feeding Habits

The black-footed ferret depends almost exclusively on prairie dogs for food and on prairie dog burrows for shelter (Hillman 1968, Biggins et al. 2006c). Recent data suggest that the diet of black-footed ferrets may be slightly more plastic than previously thought, with adult females consuming up to 33% of non-prairie dog prey (mice, voles, and other small mammals) on an annual basis (Brickner et al. 2014). The researchers suggested that adult females killed prairie dogs and provisioned them for dependent young, while meeting their own energetic demands by consuming alternate prey. In contrast, the diet of adult males and juveniles of both sexes consisted of approximately 75% prairie dogs on an annual basis. Regardless of differing food habits between sexes at different times of the year, black-footed ferrets remain highly specialized predators that are obligate associates of prairie dogs (Hillman and Clark 1980).

2.1.4 Life Cycle and Reproduction

The black-footed ferret is solitary, except for breeding and the period when mother and young are together (Forrest et al. 1985). The ferret breeds at approximately one year of age from mid-March through early April in the wild (Wilson and Ruff 1999), and adult sex ratio is approximately one male to two females (Forrest et al. 1988). Gestation is about 42–45 days and parturition (whelping) takes place below ground with an average litter size of 3.5 individuals (Wilson and Ruff 1999). The kits are born altricial (helpless and requiring parental care) and develop quickly with the black mask becoming apparent after 16-18 days, eyes opening at 37 days, and nearly reaching adult weight after 125 days (Vargas and Anderson 1996). The kits are mobile enough to appear above ground in July and are generally ready to disperse from their mother by September or October.

Dispersal, defined as a permanent movement away from the natal area, occurs in the fall months among the young of the year, although a few instances of adults making permanent moves in the fall have been recorded (Forrest et al. 1988). Dispersal distances and movements up to 49 kilometers (km) have been recorded (Biggins et al. 1999) in newly released captive born animals and dispersal of more than 20 km in wild-born ferrets. Males tend to move greater distances than females.

2.1.5 Activity Patterns

The black-footed ferret is generally a nocturnal predator, appearing above ground at irregular intervals and for irregular durations (Clark et al. 1986). In the post-breeding period ferrets tend to be most active on nights when the moon is above the horizon (Eads et al. 2012a), but ferrets have been observed during the day (Clark et al. 1986, Eads et al. 2010, Livieri et al. 2013). The ferret is an extreme specialist that depends on prairie dogs for food and shelter (Biggins et al. 2006c). Ferrets occupy prairie dog burrows and do not dig their own burrows. They will modify burrows, dig out hibernating prairie dogs or remove a soil plug in a behavior called trenching (Eads et al. 2012b).

2.1.6 Home Range and Territoriality

Black-footed ferret densities at the last known wild population near Meeteetse, Wyoming, were linearly correlated with white-tailed prairie dog colony size, with an average density of one adult ferret per 40–60 ha of occupied prairie dog habitat (Forrest et al. 1985). Information on ferret life expectancy is sparse. In the wild, females have reached 5 years of age and males have reached 4 years. However, mustelids typically have short mean life expectancies and 50 percent or greater juvenile mortality (Clark 1989). The mean life expectancy of free-ranging ferrets in the Meeteetse population was 0.9 years (Biggins et al. 2006a). Annual survival rates for the Conata Basin, South Dakota population were 70% for juvenile females, 50% for adult females and 38% for males regardless of age (McDonald et al. 2005). The juvenile age class comprises approximately 60-67% of the population and has the largest effect on population growth (Forrest et al. 1988, McDonald et al. 2005).

Black-footed ferrets generally conform to a typical mustelid spacing pattern with some overlap between female home ranges and nearly complete overlap between male and female home ranges (Powell 1979, Livieri and Anderson 2012). Ferrets select for areas within prairie dog colonies that contain high burrow densities and thus high densities of prairie dogs (Biggins et al. 2006c, Eads et al. 2011, Jachowski et al. 2011b, Livieri and Anderson 2012). Home ranges of female ferrets occupying high density black-tailed prairie dog habitat average approximately 60 ha whereas males average approximately 130 ha (Jachowski et al. 2010, Livieri and Anderson 2012). Territories, a defended area within an animal's home range, average 13 ha for females and 36 ha for males and contain higher burrow densities than the rest of the home range (Livieri and Anderson 2012).

2.2 Black-footed Ferret Needs

A species can only be viable if its basic ecological needs are satisfied. In this section, we translate our knowledge of the black-footed ferret's biology and ecology into its needs at the individual, population, and species levels. For individual black-footed ferrets, we describe the resources and habitat conditions that adults, juveniles, and kits need to complete each stage of their life cycle. We then describe the habitat and demographic conditions that black-footed ferret populations need to be resilient. Finally, we describe what the species needs in order to be viable in terms of resiliency, redundancy, and representation (Figure 3).

2.2.1 Individual Needs

As obligate predators of prairie dogs, black-footed ferrets typically need large, contiguous (≤ 7 km apart; Biggins et al. 1993) prairie dog colonies to meet their individual needs. Prairie dogs are the predominant prey taken by black-footed ferrets (Sheets et al. 1972, Campbell et al. 1987), and most explicit observations of black-footed ferrets mention prairie dog colonies (Biggins et al. 2006c). Black-footed ferrets do not excavate their own extensive burrow systems, but instead rely on the burrow systems constructed by prairie dogs for shelter (Forrest et al. 1988). Black-footed ferrets utilize prairie dog burrow systems for whelping, and young emerge aboveground at approximately 60 days of age. As juvenile black-footed ferrets disperse from their natal burrows at approximately 100 days of age, they adopt the same food habits and shelter requirements of adult black-footed ferrets.

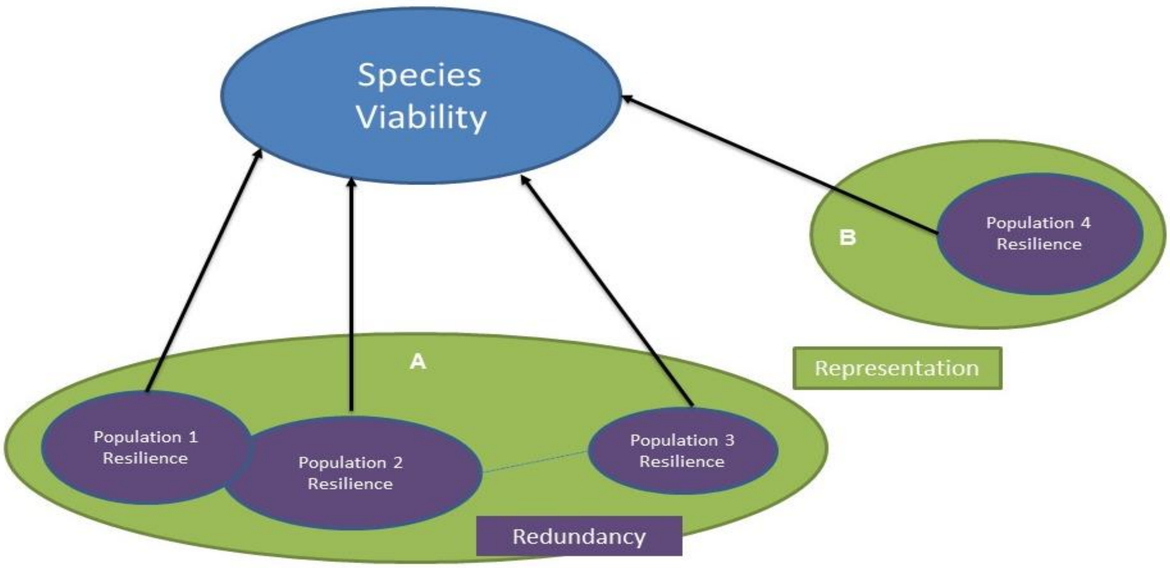

Figure 3. Illustration of how resiliency, redundancy, and representation influence what a species needs for viability.

2.2.2 Population Needs

Black-footed ferrets currently exist in the wild only at isolated reintroduction sites, which may contain both captive-bred and wild-born ferrets, may contain ferrets translocated from other sites, and are not necessarily equivalent to biological populations as they may have existed historically. Ferrets are also maintained in a captive setting at six widely separated captive rearing facilities. For the purpose of this SSA, we consider all wild (reintroduced) black-footed ferrets to constitute one “population”, and all captive black-footed ferrets to constitute another “population”. We further subdivide these populations into analysis units (subpopulations or reintroduction sites are each considered an “analysis unit” for the wild population, and each captive breeding facility is considered an “analysis unit” for the captive population). We use these terms interchangeably throughout the document. These rather simplistic definitions are an artifact of the black-footed ferret being extirpated from the wild in 1987 to initiate a captive breeding program (Lockhart et al. 2006), and subsequent occurrence in the wild for the species is the result of purposeful reintroduction efforts at discrete reintroduction sites.

The 1988 Black-footed Ferret Recovery Plan (USFWS 1988) and subsequent revisions (USFWS 2013a) established a minimum criterion of 30 breeding adults for a black-footed ferret subpopulation to count toward recovery goals. This criterion was derived from the study of the last free-ranging ferret population discovered at Meeteetse, Wyoming in 1981, which averaged approximately 25 breeding adults throughout intensive demographic studies from 1982 to 1985. Since this population apparently persisted for a considerable amount of time prior to its discovery in 1981, it was assumed that 25 breeding adults provided a stable basis for population persistence (USFWS 1988). In developing a conservative estimate of black-footed ferret habitat requirements based on known female ferret spacing (Biggins et al. 1993, 2006b), USFWS (2013a) estimated that 90 ha of black-tailed prairie dog habitat was required to support one black-footed ferret female, and 150 ha of Gunnison's or white-tailed prairie dog habitat was required to support one black-footed ferret female. Assuming a 1:2 sex ratio and overlapping male and female home ranges (Biggins et al. 1993), a population of 30 breeding adult black-footed ferrets would require 1,800 ha of black-tailed prairie dog habitat, and 3,000 ha of Gunnison's or white-tailed prairie dog habitat. Biggins et al. (1993, 2006c) describes methodologies based on bioenergetics requirements used to derive these estimates.

When individual black-footed ferrets have access to ample food and habitat (defined here as abundant prairie dog prey), the species is capable of a high reproductive rate and can readily colonize unoccupied habitat (Grenier et al. 2007). At the population level, juvenile production and survival drives black-footed ferret population growth (Forrest et al. 1988), and high juvenile production is correlated with the availability of prairie dog pups as a food resource (Biggins et al. in preparation).

Connectivity between discrete reintroduction sites encourages dispersal of individuals and maintains gene flow, which prevents extirpation due to low genetic diversity and accelerated genetic drift (Lacy 1987). Larger, less isolated subpopulations are also more resilient and less likely to be extirpated by a stochastic event (Frankel and Soulé 1981, Smith et al. 2018). Because black-footed ferrets were not widely studied prior to the onset of substantial population declines (Hillman 1968, Forrest et al. 1988) and the extirpation of the species from the wild (Lockhart et al. 2006), the importance of connectivity to the maintenance of genetic fitness is poorly understood. Given the species' obligate association with prairie dogs, it is likely that individual black-footed ferret populations associated with larger, less fragmented prairie dog colonies exhibit greater resiliency and are less likely to be extirpated by stochastic events than those associated with smaller, fragmented colonies (Miller et al. 1994, Jachowski et al. 2011a).

2.2.3 Species Needs

As a species, the black-footed ferret needs multiple resilient populations (i.e., redundancy) that display a breadth of ecological and genetic diversity (i.e., representation) across its historic range

(12 present-day states and across three species of prairie dogs; USFWS 2013a). One source suggests that the black-footed ferret needs a minimum of 20 resilient populations to meet these criteria (Lacy and Clark 1989). Since recovery of the black-footed ferret is heavily dependent on the availability of captive-reared animals for release at reintroduction sites, the sustainability of the captive breeding program and the ability to translocate wild-born black-footed ferret kits to new reintroduction sites is of utmost importance (Garelle et al. 2014). Establishment of additional reintroduction sites is key to increase both ecological and genetic diversity (representation), while meeting established recovery goals (USFWS 2013a).

The duplication and distribution of resilient black-footed ferret populations across the landscape enhances redundancy, and the presence of populations in a diversity of ecological settings (in the case of the black-footed ferrets, the presence of populations in black-tailed, Gunnison’s, and white-tailed prairie dog habitats) increases representation. Representation is also evidenced by genetic variation, and given the black-footed ferret’s very limited number of founder animals (N=7) and extirpation in the wild in 1987 (Lockhart et al. 2006), genetic representation will likely remain a challenge for the species well into the future (Wisely 2006).

2.2.4 Summary of Species Needs in terms of the 3Rs

As described above, at the individual level, the primary requirement for all black-footed ferret life stages is prairie dogs. At the population level, black-footed ferret populations need at least 30 breeding adults, which requires at least 1,800 ha of black-tailed prairie dog habitat or 3,000 ha of Gunnison’s or white-tailed prairie dog habitat (USFWS 2013a). Populations also need some level of connectivity, a sufficient rate of juvenile survival, and larger, less fragmented prairie dog colonies to maintain resiliency to stochastic events. At the species level, the black-footed ferret needs multiple (≥20), resilient populations (i.e., redundancy) that display a breadth of ecological and genetic diversity (i.e., representation) across its historic range, including black-tailed, Gunnison’s, and white-tailed prairie dog habitats. A captive breeding population is also needed to provide individuals for release at reintroduction sites, thereby increasing resiliency of those populations, and to provide additional redundancy in the case of catastrophic events that could affect reintroduction sites, as well as to maintain the genetic diversity that is needed for the species to adapt to changing conditions (representation).

Chapter 3. Influences, Historical Condition, and Current Condition

In this chapter, we summarize the historical and current conditions of the black-footed ferret at the population and species levels. To do this, we introduce the stressors that have and continue to influence the species’ condition as well as current conservation efforts which address some of these stressors. We then detail how black-footed ferret abundance and distribution has changed over time. Finally, we put the species’ historical and current conditions in the context of the 3Rs to assess its current viability. The viability of the black-footed ferret is inextricably linked with the viability of black-tailed, Gunnison’s, and white-tailed prairie dogs, as it is an obligate associate of these species. At the species level, the black-footed ferret needs multiple, resilient populations within the range of these three prairie dog species in order to be viable (Chapter 2).

3.1 Range of the Black-footed Ferret

As noted in Chapter 2, the historic range of the black-footed ferret coincided with the historic range of black-tailed, Gunnison’s, and white-tailed prairie dogs. For the purposes of this SSA, we compiled spatial data delineating the current ranges of the three species of prairie dogs in order to develop a potential range for the black-footed ferret. At present, black-footed ferrets have been purposely reintroduced at 29 discrete sites within the potential range (Figure 4). We do not expect that black-footed ferrets could occur throughout the entire potential range, as prairie dog colony size and configuration are important determinants of black-footed ferret habitat suitability (Biggins et al. 1993, Bevers et al. 1997, Biggins et al. 2006d), and unsuitable habitats for both prairie dogs and ferrets exist within the potential range as currently defined. Unsuitable habitats can include wetlands, cultivated areas, developed areas, and areas where soils and topography are not suitable for prairie dogs (Ernst et al. 2006). A more spatially refined analysis of the potential range is needed to determine where additional black-footed ferrets can potentially be established. Preliminary efforts at finer-scale analyses can be found in Luce (2006).

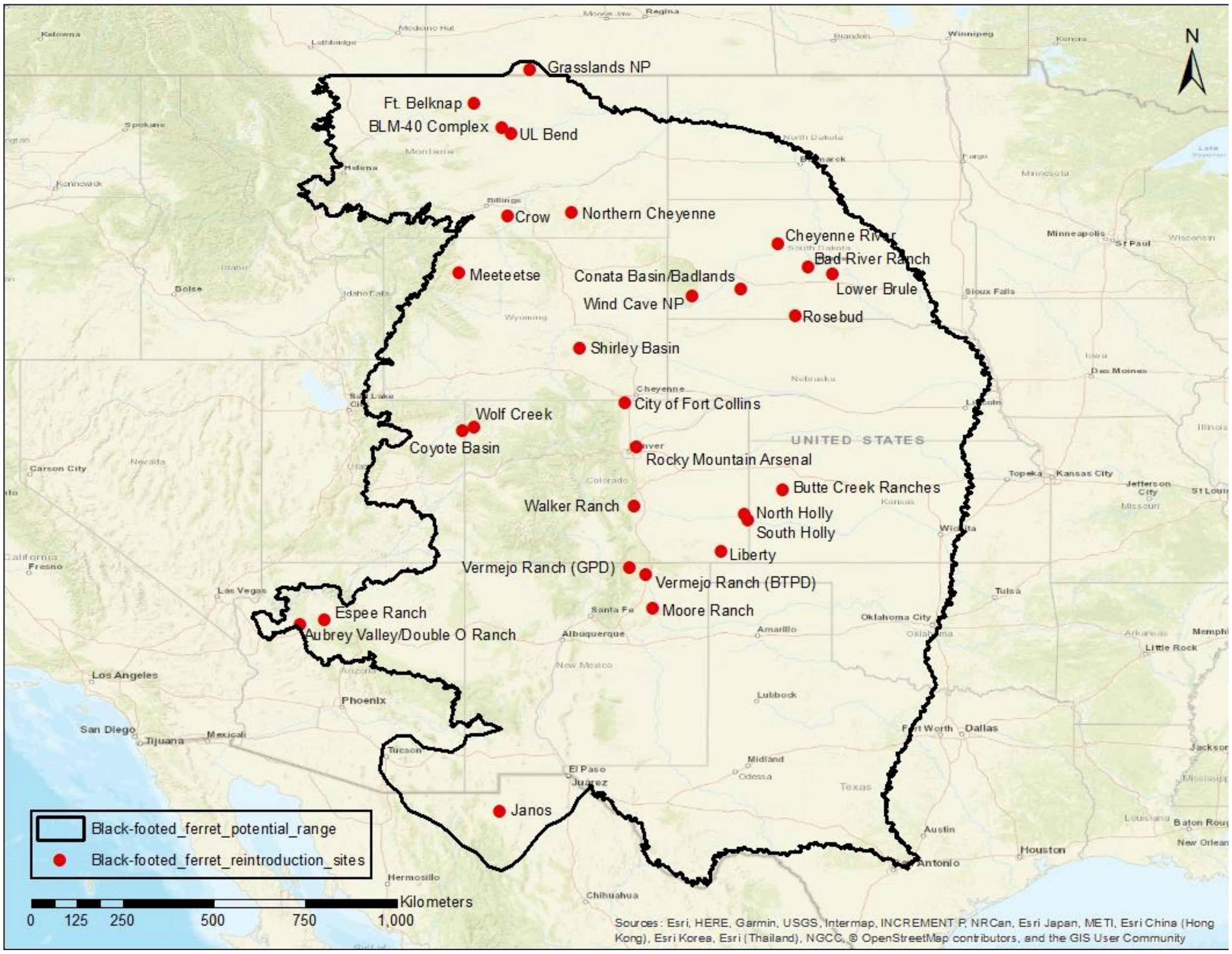

Figure 4. Black-footed ferret potential range and locations of reintroduction sites. The potential range represents the outer boundary of areas where black-footed ferrets occur or could occur, but not all areas within the potential range are occupied or provide potentially suitable habitat. The potential range encompasses approximately 231,425,000 ha.

3.2 Factors Influencing Black-footed Ferret Condition

In this section, we discuss the external factors (stressors) that may influence the 3Rs, and thus the viability, of the black-footed ferret (Figure 5). Through careful review of available literature on the black-footed ferret, black-tailed prairie dog, Gunnison's prairie dog, and white-tailed prairie dog, we chose to evaluate stressors for which there is broad consensus on the potential to affect black-footed ferret viability at the species-wide level. These include disease, genetic fitness, drought, agricultural land conversion, recreational shooting of prairie dogs, poisoning of prairie dogs, range management, urbanization, and energy development. Although the magnitude and scale of effects of these stressors varies, the importance of these stressors is supported by other recent reviews of black-footed ferret viability (USFWS 2013a, Belant et al. 2015). We did consider other possible stressors in the course of our analysis, such as predation (USFWS

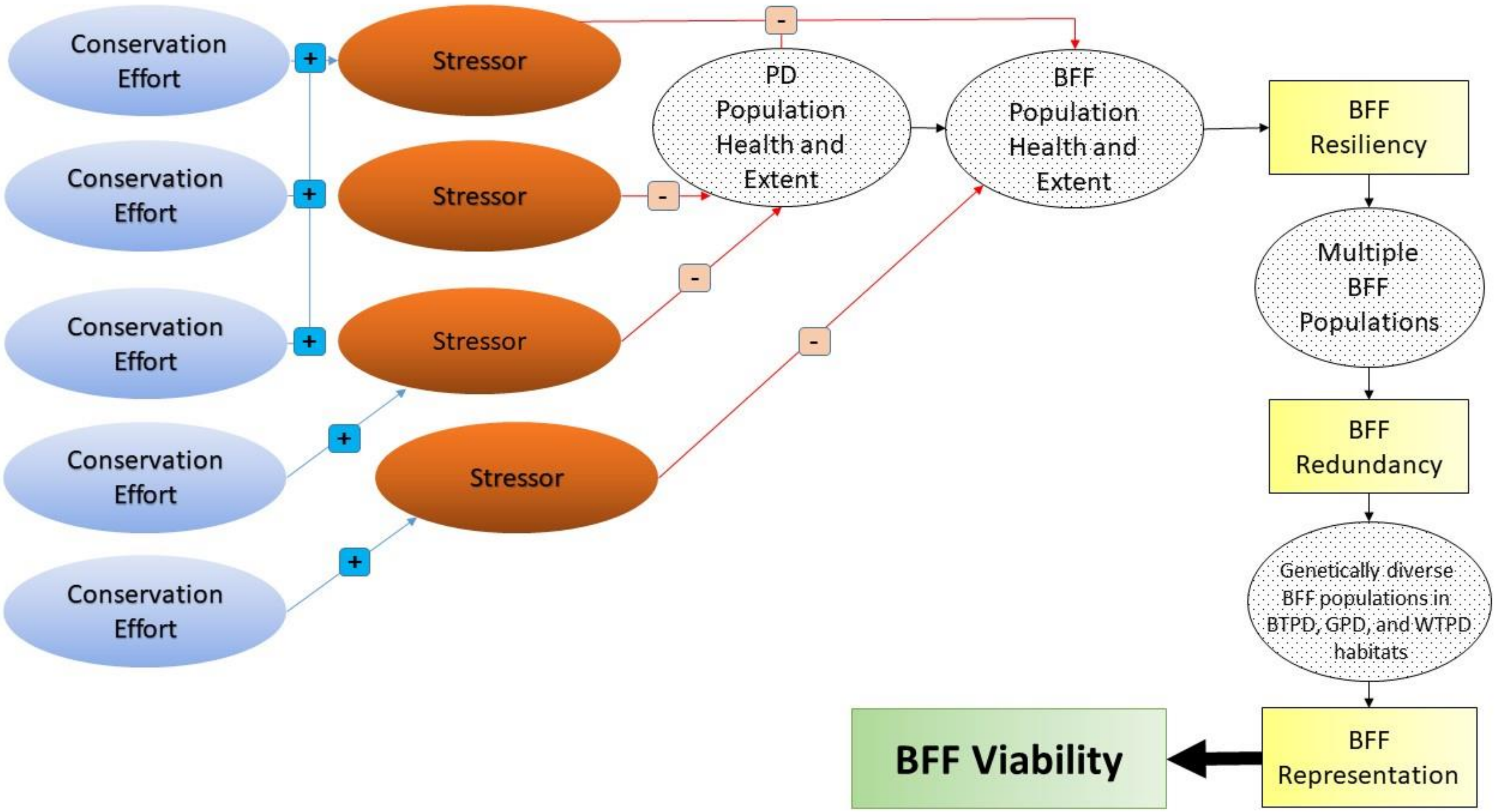

Figure 5. A general influence diagram modeling how stressors and conservation efforts can affect the resilience of black-footed ferret populations. Stressors (orange polygons) decrease the health and extent of prairie dog populations and black-footed ferret populations. Conservation efforts (blue polygons) increase both prairie dog and black-footed ferret population health, and increase black-footed ferret population resiliency. The presence of multiple resilient black-footed ferret populations that are genetically diverse and located in diverse habitat types increases redundancy and representation, and overall black-footed ferret viability.

2013a), but found no credible support that these stressors, either individually or cumulatively, could have population-level effects. We largely excluded these stressors from further analysis in this SSA report. For those factors considered further, we include a description, a current quantification of the magnitude of the stressor (if possible given the data available), and a summary of ongoing and/or potential conservation measures that may ameliorate these effects.

3.2.1 Disease

Native canine distemper and non-native sylvatic plague have seriously affected both wild and captive populations of the black-footed ferret. Several other native diseases, including coccidiosis, cryptosporidiosis, and hemorrhagic syndrome also affect captive populations (Hutchins et al. 1996), but are not common in the wild.

3.2.1.1 Canine Distemper

Description
Canine distemper can have significant adverse effects on the black-footed ferret. This disease was originally believed to have been the primary cause of the demise of the last wild population of ferrets at Meeteetse, Wyoming, in the mid-1980s (Clark 1989). At that time, it was believed that plague did not directly affect the species because many carnivore species, including other ferret species, were resistant to the disease (Cully 1993, Godbey et al. 2006). However, epizootics of both canine distemper and plague were likely responsible for the decline of the Meeteetse ferrets (Lockhart et al. 2006).

The canine distemper virus causes a systemic disease that is highly virulent to carnivore species, including the black-footed ferret. It is endemic in the United States and initially challenged the reintroduction of ferrets (Wimsatt et al. 2006). Efforts in 1972 to breed ferrets from the Mellette County, South Dakota population were ultimately unsuccessful due to vaccine-induced canine distemper. Although safe in domestic ferrets, the vaccine induced fatal distemper in four of six vaccinated black-footed ferrets that were removed from the wild Mellette County population for captive breeding purposes (Lockhart et al. 2006). Some ferrets in the Meeteetse population also succumbed to distemper in the mid-1980s (Clark 1989). Today, an effective commercial distemper vaccine is widely employed in both the captive and reintroduced ferret populations (Marinari and Kreeger 2006). Canine distemper vaccination can substantially reduce the threat of catastrophic population losses of ferrets. However, it is not practical to vaccinate all wild-born ferrets to protect them from periodic distemper events. Accordingly, wild populations may require monitoring and periodic augmentation.

Summary of Effects on the 3Rs
While canine distemper was partially responsible for the decline in the last free-ranging black-footed ferret population in Meeteetse, WY, in 1985, no canine distemper epizootics have been

observed since reintroduction efforts began in 1991 (USFWS 2016a). Due to its reduced prevalence and vaccination efforts in both wild and captive settings (USFWS 2016a, USFWS 2017), at present canine distemper does not appreciably affect black-footed ferret resiliency, redundancy, and representation.

Current and Suggested Conservation Measures
Vaccination of captive and wild-born black-footed ferrets has proven to be a useful strategy to prevent canine distemper epizootics, although limited resources prevent more intensive monitoring to assess its effectiveness in the wild (Wimsatt et al. 2006, USFWS 2016a, USFWS 2017). Care must be taken to select the appropriate vaccines for this disease, as mortalities have occurred through the use of modified-live vaccine constructs (Wimsatt et al. 2006, USFWS 2017).

3.2.1.2 Sylvatic Plague

Description
Sylvatic plague infections are caused by the bacterium *Yersinia pestis*. Fleas acquire the bacterium from biting infected animals and can then transmit it to other animals in a similar manner. The disease can also be transmitted pneumonically (via the respiratory system) among infected animals or via the consumption of contaminated tissues (Godbey et al. 2006, Abbott and Rocke 2012). Recovery efforts for the black-footed ferret are hampered because both ferrets and prairie dogs are extremely susceptible to plague (Barnes 1993, Gage and Kosoy 2006). Plague can affect ferrets directly via infection and subsequent mortality. It can also indirectly affect ferrets through the disease's effects on prairie dogs and the potential for dramatic declines in the ferret's primary prey base (Barnes 1993, Biggins and Kosoy 2001).

Sylvatic plague did not exist on the North American continent prior to 1900, when it was inadvertently introduced into San Francisco (Gage and Kosoy 2006). It was first observed in prairie dogs in 1932 in Arizona (Cully 1993) and detected in all states within the historical range of the black-footed ferret by 2005 (Abbott and Rocke 2012). The disease is currently present throughout the entire range of white-tailed and Gunnison's prairie dogs and in at least the western two-thirds of the range of black-tailed prairie dogs (Barnes 1993, Lockhart et al. 2006, Abbott and Rocke 2012). In addition, plague is very likely to be present in many counties where it has not yet been documented (Biggins 2013).

Sylvatic plague can be present in a prairie dog colony in either an enzootic (persistent, low level of mortality) or epizootic (swift, large-scale die-offs) state. Most of the information we have regarding effects from plague has been collected during epizootic events. However, two recent studies have expanded our understanding of enzootic plague and its effects on black-footed ferret recovery. In Montana, black-footed ferret survival significantly improved when plague vaccinations (Rocke et al. 2006, Rocke et al. 2008) were given to ferrets or when the insecticide deltamethrin was applied as a prophylactic treatment (Seery et al. 2003, Seery 2006) to control fleas in prairie dog burrows. These results were achieved even in the absence of a discernable die-off of prairie dogs (Matchett et al. 2010). The researchers concluded that increased ferret mortality associated with enzootic plague was hindering ferret recovery and fleas were a key component in transmission. A wider-scale study using prophylactic deltamethrin treatments in Montana and Utah (Biggins et al. 2010) suggested that the enzootic phenomenon was present in black-tailed prairie dogs, white-tailed prairie dogs, and Utah prairie dogs, and that vector control improved the survival of all three prairie dog species.

The factors responsible for the eruption of epizootics and the maintenance of enzootic plague are not well understood. Researchers have identified prairie dog density (Cully and Williams 2001), colony connectivity (Savage et al. 2011), landscape composition (Johnson and Collinge 2004, Collinge et al. 2005, Brinkerhoff et al. 2010), other organisms functioning as short-term reservoirs (Webb et al. 2006, Markman et al. 2018), and local climatic conditions (Snall et al. 2008, Eads and Biggins 2017) as potential influential factors. Regardless of the mechanism (or more likely, combination of mechanisms) involved, sylvatic plague remains an important disruptor of prairie ecosystems (Eads and Biggins 2015, Biggins and Eads 2019).

Summary of Effects on the 3Rs

In general, larger populations exhibit higher resiliency and are better able to withstand stochastic events. While canine distemper epizootics are relatively rare and occur in localized settings (Williams and Thorne 1996), the likelihood of entire populations of black-footed ferrets being extirpated during sylvatic plague epizootics is high (Shoemaker et al. 2014), and the effects of plague can be exacerbated by other stressors such as drought and recreational shooting (see **Sections 3.2.2 and 3.2.4**, below). Further, stressors such as drought and recreational shooting can create positive feedback loops where the effects of plague are magnified (Biggins and Eads 2019). The loss of individual populations due to plague reduces redundancy and representation, particularly if populations occurring in different habitat types (e.g., black-tailed, Gunnison's, and white-tailed prairie dogs) succumb to plague simultaneously. Given the black-footed ferret's low level of genetic diversity, plague represents an additive stressor that further diminishes the species' ability to adapt to changing environmental conditions (Wisely et al. 2002).

Current and Suggested Conservation Measures

Current plague management efforts aim to minimize the effects of plague on black-footed ferrets by reducing flea loads on prairie dogs through vector control, immunizing individual black-footed ferrets against the disease, immunizing individual prairie dogs against the disease, or a combination of these strategies. Applying the insecticide deltamethrin to individual prairie dog burrows ("dusting"; Seery et al. 2003, Seery et al. 2006) effectively reduces flea loads and increases both prairie dog and black-footed ferret survival by reducing the likelihood and rate of plague transmission (Godbey et al. 2006, Biggins et al. 2010, Matchett et al. 2010). Drawbacks to dusting include effects to non-target invertebrates and high labor and materials costs

(Jachowski et al. 2011c). Flea resistance to deltamethrin has also been documented at sites where the insecticide has been applied on an annual basis for < 10 years (Eads et al. 2018), and managers should attempt to utilize other products using an integrated pest management paradigm so that resistance issues can be avoided (Eads and Biggins 2019). A potential new plague mitigation product is the systemic pulicide fipronil. When incorporated into grain baits, researchers found significant short-term control of fleas (3 months) in black-tailed prairie dog colonies in Colorado and South Dakota (Poche et al. 2017, Eads et al. 2019). The cost of this product is equivalent to that of deltamethrin dusting, and while in theory its non-target effects should be lower (Borchert et al. 2009), additional evaluation is needed in this regard.

Rocke et al. (2006) developed a vaccine (F1-V) to prevent plague in black-footed ferrets. Ferrets immunized by a series of two subcutaneous injections had significantly higher antibody titers than un-immunized animals. Eleven of 16 vaccinated individuals survived when challenged with plague 6 months after immunization. All eight control animals died. The 11 survivors were again challenged by ingestion of a plague-infected mouse 2 months later and all survived. The F1-V vaccine is now used operationally (Abbott and Rocke 2012, USFWS 2016a), and most captive ferrets, including all of those provided for reintroduction, are currently vaccinated for plague. Many ferret kits at the Conata Basin-Badlands reintroduction site and several other reintroduction sites are also vaccinated annually in an effort to minimize effects from the ongoing plague epizootic. Recent experience at this site indicates that dusting alone is insufficient to maintain ferret populations during a plague epizootic and that vaccination increases the survival of ferrets on dusted colonies; without both dusting and vaccination the population at Conata Basin-Badlands would likely have perished (Livieri 2019). However, maximum protection is difficult to achieve in wild ferrets, which must be trapped twice, two to four weeks apart, to receive two effective doses of the vaccine.

Another vaccine under development, the sylvatic plague vaccine (SPV), is delivered via treated baits to prairie dogs, and may eventually be useful in protecting ferrets from habitat reduction due to plague. This vaccine has been effective in a laboratory setting (Rocke et al. 2010, Abbott and Rocke 2012), and a recent broad-scale experiment involving four species of prairie dogs to test effectiveness in the field found that SPV prevented complete colony collapse in instances where plague epizootics were documented (Rocke et al. 2017). However, some prairie dogs on these colonies still died from plague because researchers were not able to attain either a 100% vaccination rate or a sufficient vaccination response to impart herd immunity (Rocke et al. 2017).

In a black-tailed prairie dog population in Colorado, the effectiveness of SPV was found to be highly influenced by temporal variation in treatment, as well as temporal variation in the eruption of plague epizootics (Tripp et al. 2017). The authors found that neither dusting nor SPV provided colonies with complete protection, but repeated annual application of SPV well in advance (> 30 days) of a plague epizootic stabilized survival rates in adult prairie dogs exposed to an epizootic. To maximize effectiveness, Tripp et al. (2017) suggested that SPV should be applied in non-epizootic conditions, and should be administered over large, contiguous areas in late summer or fall to ensure vaccination of juvenile prairie dogs. Further research is needed to determine if SPV can limit plague transmission by limiting the role of prairie dogs as a reservoir, and if it is an effective means of mitigating the overall effects of sylvatic plague on black-footed ferrets and associated species.

Vector control (i.e., dusting and/or fipronil grain baits) and SPV use in conjunction with vigilant plague epizootic monitoring may provide the most effective way to reduce the range-wide effects of plague (Antolin et al. 2002, Abbott et al. 2012, Tripp et al. 2017). However, the widespread use of these prophylactics across the species' range is logistically and financially challenging. To address this concern, a new method of manufacturing has made SPV bait production quicker and more cost effective (Corro et al. 2017), and recent tests have explored the utility of using drones and all-terrain vehicles equipped with mechanical dispensers to distribute SPV over larger areas (USFWS 2016b). These technologies are also being used to develop application techniques for other plague management practices, such as the application of systemic insecticides (Matchett 2019). Information provided by recent studies on plague management techniques may help managers gain the most benefit from limited, but targeted, conservation efforts. Vaccination rates of 50 to 80 percent of individuals in a colony using SPV may be necessary to control plague epizootics (Tripp et al. 2014). Broadcasting SPV-laden baits at high densities during the fall, as opposed to the spring, may be the best way for managers to reach these vaccination goals (Tripp et al. 2014, Tripp et al. 2017).

While the goal of vector control practices such as dusting should be to dust entire colonies for maximum plague prevention, dusting even a portion of a colony can buffer it against the effects of a plague epizootic for some time (Tripp et al. 2017). Flea abundance rebounded to high levels 12 months after dusting treatment on plots that were adjacent to large blocks of untreated habitat, so managers may consider dusting more frequently or at least annually to effectively suppress plague on small, disjunct colonies in larger habitat areas; however, in some instances dusting provided significant flea reduction for up to two years (Eads and Biggins 2019). A single dusting event on an entire colony would theoretically suppress flea abundance for a longer period of time. Preventative dusting is also more effective than dusting in response to an observed plague epizootic (Tripp et al. 2016).

Plague management activities including vector control and SPV distribution are ongoing at most, but not all, black-footed ferret reintroduction sites (Table 1). Intensive, long-term plague management has occurred at the Conata Basin-Badlands reintroduction site in South Dakota since 2008, when epizootic plague was first documented (USFWS 2013a). Prior to the epizootic, Conata Basin-Badlands had provided a surplus of kits for translocation to other reintroduction sites since 2000 (Livieri 2006). Plague was detected in prairie dogs approximately 40 km south

Table 1. Summary of plague management activities at black-footed ferret reintroduction sites, 2014-2018.

Site Name and Location*	**Size in 2018 (ha)**	**2014 dusting (ha)**	**2015 dusting (ha)**	**2016 dusting (ha)**	**2016 SPV (ha)**	**2017 dusting (ha)**	**2017 SPV (ha)**	**2018 dusting (ha)**	**2018 SPV (ha)**
Conata Basin-Badlands, SD	5,494	4,446	4,282	3,418	405	3,589	405	3,399	411
UL Bend NWR, MT	202	0	0	0	486	0	486	0	364
Aubrey Valley/Double O Ranch, AZ	26,485	0	0	0	0	0	0	256	248
Ft. Belknap Reservation, MT	688	0	157	116	0	116	0	75	0
Coyote Basin, CO/UT	10,117	0	0	0	0	0	0	0	1,214
Lower Brule Reservation, SD	723	0	101	267	0	0	0	0	506
Wind Cave National Park, SD	739	0	207	102	0	98	0	243	486
Espee Ranch, AZ	8,811	0	0	0	0	0	0	65	251
Northern Cheyenne Reservation, MT	324	0	0	0	0	401	0	9	0
Grasslands National Park, SK	769	0	472	139	0	101	0	351	0
Walker Ranch, CO	340	0	0	405	0	293	293	0	340
City of Fort Collins, CO	746	1,000	1,000	622	0	405	676	405	693
North Holly, CO	55	0	728	1,012	0	66	55	0	55
Liberty, CO	93	0	304	142	0	16	32	0	93
Rocky Mountain Arsenal NWR, CO	1,214	0	1,046	809	405	1,212	405	0	615
Crow Reservation, MT	1,985	N/A	525	710	0	470	0	221	0
South Holly, CO	120	N/A	0	607	0	93	101	0	81
Meeteetse, WY	2,236	N/A	N/A	2,032	0	1,165	0	1,189	405
Bad River Ranch, SD	121	N/A	N/A	N/A	N/A	364	253	61	6
Moore Ranch, NM	164	N/A	N/A	N/A	N/A	N/A	N/A	0	164
TOTALS	**61,426**	**5,446**	**8,822**	**10,381**	**1,296**	**8,389**	**2,706**	**6,274**	**5,932**

*Sites shown in italics are no longer occupied by black-footed ferrets as of 2018 of Conata Basin in 2005. Approximately 1,600 kilograms (kg) were dusted on 2,800 ha of prairie dog colonies in known ferret habitat during the late summer and fall of 2005 in an effort to control fleas. Despite continued dusting efforts, plague was identified at Conata Basin in May 2008.

Following detection of plague at Conata Basin-Badlands, several Federal agencies undertook a dusting effort that targeted approximately 4,000 ha of prairie dog colonies (Griebel 2008). Approximately 4,000 ha of untreated prairie dog colonies were affected by plague (Griebel 2008). Plague in Conata Basin-Badlands continued into 2009 and removed approximately 2,000 additional hectares of prairie dogs for a two-year reduction in occupied prairie dog habitat from 12,600 ha to 6,500 ha (Griebel 2009). Dusting at Conata Basin-Badlands has continued annually to the present. The Conata Basin-Badlands reintroduction used dusting and vaccination to actively manage black-footed ferret habitat in the midst of this plague outbreak and have maintained approximately 4,455 ha of prairie dog colonies occupied by ferrets (Griebel 2009). The precise extent of ferret mortality at Conata Basin is not known, but is presumed to be as much as 75 percent of the pre-epizootic population, based upon survey data and the number of acres affected at this site (USFWS 2013a).

In one instance, black-footed ferrets appear to have prospered despite the prior presence of plague. In 1991, Shirley Basin, Wyoming, was the first site where ferrets were reintroduced. White-tailed prairie dogs occupy this site. Ferret releases at Shirley Basin were suspended in 1994 due to prairie dog population declines caused by plague. By 1997, only five ferrets were observed (Grenier et al. 2007). However, 52 ferrets were observed in 2003 and thereafter, the Shirley Basin ferret population received additional augmentation of captive-born animals and grew rapidly (Lockhart et al. 2006, Grenier et al. 2007). White-tailed prairie dog complexes are less densely populated than typical complexes of black-tailed or Gunnison's prairie dogs, and some authors have suggested that prairie dog colony size and density play a key role in determining the severity and duration of plague epizootics (Cully 1989, Cully and Williams 2001, Collinge et al. 2005). It is possible that scattered populations of prairie dogs avoided contracting plague and were able to sustain a small ferret population. However, ferrets and white-tailed prairie dogs at other reintroduction sites have been continuously or repeatedly affected by plague (Holmes 2008, McDonald et al. 2011), and recent research suggests that vector densities rather than host densities may be the most important factors in determining plague transmission rates (Biggins and Eads 2019).

Despite ongoing plague mitigation efforts at several black-footed ferret reintroduction sites, plague remains the most significant challenge to ferret population resiliency. Frequent, successive plague epizootics, as well enzootic plague, prevent both prairie dog and ferret populations from reaching their biological potential (Augustine et al. 2008, Eads and Biggins 2015). Ameliorating the effects of plague on black-footed ferrets and the prairie dog population that they rely upon will require rangewide, strategic use of available plague management tools (Tripp et al. 2017).

3.2.2 Genetic Fitness

Description

Genetic fitness of the black-footed ferret has been a concern in the captive breeding program due to the extreme bottleneck that the species experienced (Groves and Clark 1986, U.S. Fish and Wildlife Service 1988, CBSG 1992, Hutchins et al. 1996, CBSG 2004, Garelle et al. 2006, Howard et al. 2006, Wisely 2006). The current captive breeding program began with the genetic equivalent of seven founder animals from the last wild population at Meeteetse, Wyoming (Hutchins et al. 1996, Wisely 2006). The magnitude of loss of genetic fitness was exacerbated by the especially isolated nature of this last population, which is located on the periphery of the historical ferret range and was likely a refugium during the last glacial period that subsequently remained isolated (Wisely 2006). Both natural history (especially limited dispersal capabilities relative to other carnivores) and the ebb and flow of Pleistocene glaciers likely served to induce genetic drift within black-footed ferret populations, which created marked genetic differentiation among populations (Wisely et al. 2002).

Two types of genetic effects can affect a population's survival and overall genetic fitness: (1) inbreeding depression, caused by increased genetic homozygosity (uniformity) and the subsequent expression of deleterious genes; and (2) genetic drift, the random loss of genetic diversity in small populations (Clark 1989). In some species, genetic diversity of less than 90 percent of that in founder populations has been associated with compromised reproduction due to low birth weights, small litter size, and high neonatal mortality (Soulé et al. 1986). Genetic diversity in the current black-footed ferret population is estimated to be 85.66 percent of that in the founder population, with an average loss of 0.17 percent per year (Graves et al. 2018). A primary goal of the SSP® is to optimize genetic management of the captive population by maintaining 80 percent of the genetic diversity present in the founder population for the next 25 years (Marinari and Kreeger 2006). Some periodic abnormalities observed in captive ferrets (renal aplasia and kinked tails) may be a result of inbreeding (Hutchins et al. 1996, Howard et al. 2006), and more recently researchers have noted decreasing sperm motility and an increasing incidence of sperm structural abnormalities in the captive ferret population (Santymire et al. 2019). These abnormalities appear to be associated with inbreeding, and may be partially responsible for declining reproductive success in the captive population (Santymire et al. 2019).

The genetic uniformity of the black-footed ferret is unprecedented and rivaled by perhaps only one other carnivore, the African cheetah (*Acinonyx jubatus*) (Wisely 2006). However, carnivores typically have less genetic diversity than other mammalian taxa (Kilpatrick et al. 1986). Felines are more susceptible to inbreeding than most taxa (Wisely 2006), and yet the cheetah continues to survive in the wild. The use of artificial insemination in ferret captive breeding programs has been effective and has helped preserve genetic diversity from an underrepresented male lineage (Howard et al. 2006). Approximately 9,300 ferret kits have been produced at captive breeding facilities to date (Graves et al. 2018). Wild ferret populations appear to flourish despite reduced genetic diversity where ample plague-free habitat exists, likely due to behavioral responses linked to inbreeding avoidance (Wisely 2006). In a comparison of three reintroduction sites, Wisely et al. (2008) found that two sites (Aubrey Valley, AZ and Conata Basin-Badlands, SD) maintained similar genetic diversity as the captive population due to rapid population growth after population augmentation ceased (Conata Basin-Badlands) and annual augmentation from the captive population (Aubrey Valley). One population (Shirley Basin, WY) did experience a loss of genetic diversity and concomitant morphological changes due to a lack of augmentation and a population decline attributed to a sylvatic plague epizootic (Wisely et al. 2008). Through periodic population augmentation efforts, the black-footed ferret will likely persist with continued careful management of remaining genetic resources (Wisely 2006), although stressors such as sylvatic plague and other stochastic processes associated with small populations may create periodic bottlenecks that result in the loss of genetic diversity (Wisely et al. 2008).

Successful reproduction has been documented in black-footed ferrets at almost all reintroduction sites. In 1999, a study detected no difference in genetic diversity between captive-reared releases and their wild descendants at the UL Bend, Montana and Conata Basin-Badlands, South Dakota reintroduction sites (Wisely 2006), although the molecular-based techniques used in this study may not adequately assess short-term changes in genetic diversity (Morin et al. 2009). Additionally, ferrets at Conata Basin were able to maintain genetic diversity levels after releases of captive-reared animals ceased (Cain et al. 2011). Nevertheless, the translocation of wild-born ferrets that have been exposed to natural selection processes that do not occur in captivity may aid overall recovery and is utilized at some new reintroduction sites. Ferret reintroduction efforts have emphasized releasing captive-bred animals to the wild as quickly as possible, but also have encouraged the translocation of wild-born ferrets to initiate new recovery sites (USFWS 2013a).

Summary of Effects on the 3Rs

Reduced genetic fitness is the result of increased inbreeding and declining genetic diversity, which causes inbreeding depression and the expression of deleterious alleles (Frankel and Soulé 1981). This can cause a reduction in individual animal fitness, which can reduce the ability of a species to adapt to changing environments (Hoffman et al. 2003), or representation. Reduced genetic fitness may therefore reduce the resilience of black-footed ferret populations, and redundancy in turn is reduced if the establishment of new populations is curtailed. Reduced genetic fitness also reduces representation, as the extant populations of black-footed ferrets can trace their lineage to only seven founder animals from one geographically isolated population. Collectively, these factors serve to reduce the overall viability of the black-footed ferret.

Current and Suggested Conservation Measures

Given the black-footed ferret's history of near-extinction and the resultant small founder captive breeding population, conservation measures have emphasized retention of remaining genetic diversity through the use of the mean kinship strategy augmented by line breeding (Ballou and Oakleaf 1989). This strategy, implemented whenever logistically feasible, selects breeding pairs that maximize the representation of the most unrepresented founders of the captive population. These efforts have largely been successful, and molecular-based estimates have shown no loss in allelic diversity from the founder population to the present day captive population (Wisely et al. 2003). However, molecular-based estimates may not adequately predict short timescale changes in genetic diversity (Morin et al. 2009), and as a result, uncertainty exists as to the magnitude of the loss of genetic fitness experienced by the reintroduced black-footed ferret population. Wisely et al. (2015) state that given the small size of the reintroduced black-footed ferret population and declining genetic fitness, a productive captive population will be needed for at least the next 50 years while suitable habitat is restored and additional reintroduction sites are developed.

Despite the success in establishing and maintaining both captive and reintroduced black-footed ferret populations, conservation and possibly expansion of genetic diversity remain important considerations in black-footed ferret recovery efforts. Wisely et al. (2015) suggested that the black-footed ferret could serve as a case study to evaluate the effectiveness of interspecies somatic cell transfer (iSCNT), and efforts are underway to evaluate extant genetic material to use for these purposes (USFWS 2018a). By enabling the production of individuals via reproductive cloning using cells other than germ cells, iSCNT could help address the persistent erosion of genetic diversity via genetic drift, and may extend the useful life of the captive black-footed ferret population by incorporating genetic material from two cryopreserved founder animals from the Meeteetse population not represented in the current captive population (Wisely et al. 2015).

3.2.3 Drought

Description

Drought is defined as a deficiency in precipitation over an extended period, which reduces water supply, water quality, and range productivity, and affects social and economic activities (Woodhouse and Peck 1998, National Weather Service 2008). Although drought is recognized as a normal process, and local conditions may vary from year to year, the western United States overall has been in what is characterized as a significantly harsh drought in recent years (Woodhouse and Peck 1998; National Oceanic and Atmospheric Administration (NOAA) 2018). The last time the western United States experienced a "megadrought" of this magnitude was in the latter half of the 16th century (Woodhouse and Peck 1998). Recent studies of Gunnison's prairie dog and black-tailed prairie dog colonies have attributed observed decreases in body condition, reproductive rates, and adult and juvenile survival to the recent drought period (Facka et al. 2010, Davidson et al. 2014, Stephens et al. 2018).

Reduced precipitation due to drought decreases primary productivity and limits the amount of succulent vegetation available to prairie dogs, which in turn negatively affects obligate predators such as the black-footed ferret. Increased primary productivity at a site leads to higher prairie dog densities, increased mating success, and larger litters (Hoogland 2001). Additionally, abundant vegetation allows hibernating prairie dog species such as white-tailed prairie dogs to accumulate the large amounts of fat they need to survive hibernation (Seglund et al. 2006). Prairie dogs may become dormant or enter hibernation as early as July in dry years, extending the time they spend underground (Tileston and Lechleitner 1966, Clark 1977, Andelt et al. 2009). If hibernating prairie dogs do not have access to high quality forage and do not build sufficient fat stores prior to hibernation, they may emerge from their burrows during the winter and die from starvation (Seglund et al. 2004). For non-hibernating prairie dog species such as the black-tailed prairie dog, lack of abundant vegetation can suppress reproduction and decrease juvenile survival rates (Facka et al. 2010, Stephens et al. 2018). Since black-footed ferrets preferentially prey on prairie dog pups to feed their young at critical times of the year (Biggins et al. 2019 in preparation), factors negatively affecting prairie dog reproduction have similar effects on ferrets.

The effects of drought on the frequency and severity of plague are complex and difficult to assess. Researchers have hypothesized contradictory effects of drought on plague epizootics, with studies concluding that drought may contribute to decreased (Parmenter et al. 1999, Stapp et al. 2004, Snäll et al. 2008, Snäll et al. 2009) or increased incidences of plague (Eads and Hoogland 2016, Eads et al. 2016). In wet years or areas, flea abundance can increase due to higher primary productivity and increased soil moisture, leading to increased plague risk for a prairie dog colony (Parmenter et al. 1999, Snäll et al. 2008). In contrast, low primary productivity associated with dry years or areas can lead to decreased prairie dog body condition, increased flea loads, and higher plague risk (Eads and Hoogland 2016, Eads et al. 2016). The complex interplay of annual precipitation variability over multiple years, primary productivity, and prairie dog densities may ultimately explain colony vulnerability to plague epizootics (Eads and Biggins 2017). More research is needed to better understand how precipitation, or lack thereof, influences the frequency of plague epizootics (Eads and Biggins 2017).

Summary of Effects on the 3Rs

As an obligate predator of prairie dogs, the effects of stressors such as drought have cascading effects on the black-footed ferret. Prairie dog populations affected by drought exhibit lower abundance, reproduction, and survival. This makes both prairie dog and black-footed ferret populations less resilient and more vulnerable to other stochastic events. If drought decreases the density of individual prairie dog colonies and reduces the availability of suitable dispersal corridors, black-footed ferrets are forced to range farther during foraging activities, which negatively affects their survival and overall population resiliency. Such populations will also exhibit decreased resiliency through the limitation of immigration and gene flow. This combination of factors can lead to the loss of populations across the range and decrease the redundancy of the species, making it more susceptible to wide scale, catastrophic events. The effects of drought may be amplified if it occurs in concert with other stressors, such as a plague epizootic (Seglund et al. 2006, Lupis et al. 2007, Eads et al. 2016).

Current and Suggested Conservation Measures

We are not aware of any ongoing conservation measures involving prairie dogs, black-footed ferrets, and drought. Ensuring that prairie dog habitat is in high condition may help buffer colonies from additional vegetation losses due to drought (Seglund et al. 2006). High condition habitat is free from invasive weeds and has appropriate grazing utilization levels (Mack et al. 2017). In non-drought years, moderate grazing and the use of prescribed fire may help achieve these habitat conditions. In extreme cases, supplemental feeding by managers may help colonies persist during periods of extended drought (Davidson et al. 2014)

3.2.4 Agricultural Land Conversion

Description

Agricultural land conversion is the change in land use from a previous use to an agricultural use, including cropland and pastureland (single-species plantings grown for livestock grazing and/or hay production). At a large scale, agricultural land conversion represents a permanent loss of habitat for black-footed ferrets and their prairie dog prey (Knowles 2002, Ceballos et al. 2010). However, its effects on ferrets and prairie dogs may be mixed. In some instances, agricultural lands can benefit prairie dogs by providing a source of highly nutritious forage (Crocker-Bedford 1976, Seglund 2002, Seglund and Schnurr 2010). Roads and fences associated with agricultural conversion can fragment contiguous prairie dog habitat (Seglund and Schnurr 2010), but it is possible that agricultural lands sometimes facilitate prairie dog dispersal (Sackett et al. 2012).

Since the largest portion of the black-footed ferret's historic range occurred in black-tailed prairie dog habitat (approximately 84%; Ernst 2006), agricultural conversion in these habitats constitutes the largest loss of potential black-footed ferret habitat. Due to an abundance of deep, relatively level soils, black-tailed prairie dog habitat experienced higher levels of agricultural land conversion than other habitat types within the black-footed ferret's potential range (Choate et al. 1982, Clark 1986), but we do not have information to quantify how much potential habitat was actually lost. In addition, colonies near crops and rangelands with high domestic livestock stocking rates may be subjected to more lethal control efforts than those that are not (Hoogland 2001, Knowles 2002).

Summary of Effects on the 3Rs

Although cropland and pastureland in the United States increased from 2007 to 2012, in the longer term there has been a large decrease in the amount of land being used for agricultural production since 1980. This may reflect changes related to urbanization, energy production, as well as the increase in land retirement programs (NRCS 2015; numbers do not include Federally-owned lands). While most extant prairie dog colonies are not large or contiguous enough to support black-footed ferrets at this time, the amount of available remaining habitat is likely sufficient to sustain ferret populations (USFWS 2013a) that could be resilient. If agricultural land conversion rates do not increase, redundancy of black-footed ferret populations should not be affected. Since agricultural land conversion is less of a concern in Gunnison's and white-tailed prairie dog habitat (USFWS 2013a), representation likewise should not be affected. In summary, at present agricultural land conversion does not constitute a significant stressor with regard to black-footed ferret resiliency, redundancy, and representation.

Current and Suggested Conservation Measures

While restoration activities to restore former cropland to prairie dog habitat are uncommon, the practice has occurred in some areas (Truett et al. 2006, USFWS 2013b). More relevant to the conservation of prairie dog habitat are attempts to minimize conflicts with agriculture and the development of incentive programs to increase prairie dog tolerance (Seglund and Schnurr 2010, NRCS 2014). Such conservation and incentive efforts are often at odds with state and local laws that mandate prairie dog control (Kansas Statutes Annotated 80-1201 and 80-1203), making them difficult to implement at the scale needed for black-footed ferrets. Conservation efforts may be more effective if they are focused on remaining occupied prairie dog habitat rather than restoration of former croplands, since cropland conversion no longer appreciably reduces survival of reintroduced ferrets contributing to recovery goals for the species (USFWS 2013a).

3.2.5 Recreational Shooting of Prairie Dogs

Description

Several species of prairie dogs are subjected to shooting as recreation and as a form of pest management. Depending on its intensity, shooting can negatively affect local prairie dog populations (Knowles 1988, Vosburgh and Irby 1998, Keffer et al. 2001), and the resulting loss in prey base likely affects black-footed ferret reintroduction sites (Pauli 2005, Reeve and Vosburgh 2006). These effects are more pronounced in black-tailed prairie dog colonies due to their higher densities and greater accessibility to shooters relative to Gunnison's and white-tailed prairie dog colonies (Reeve and Vosburgh 2006). Recreational shooting is potentially more of an additive source of mortality in black-tailed prairie dog colonies for these reasons (Reeve and Vosburgh 2006).

At the Conata Basin-Badlands reintroduction site, prior to the establishment of shooting closures within the designated ferret recovery area, an estimated 75 percent of the prairie dog population was reduced in density and areal extent by recreational shooting (USFWS 1998). Recreational shooting not only reduces the number of prairie dogs in a colony, but also decreases prairie dog density (Knowles 1988), occupied acreage (Knowles and Vosburgh 2001), and reproduction (Stockrahm 1979). Juvenile and adult female prairie dogs are more susceptible to recreational shooting than adult males (Vosburgh and Irby 1998, Keffer et al. 2001), which can negatively affect black-footed ferret habitat quality due to the species' reliance on prairie dog pups as a food source (Biggins et al. 2019 in preparation). Recreational shooting of prairie dogs also leads to increased rates of emigration (Keffer et al. 2001).

In addition to indirect effects on black-footed ferrets, recreational shooting also causes direct mortality to prairie dog associated species (Knowles and Vosburgh 2001). Thus, incidental take of black-footed ferrets by prairie dog shooters is also a potential, but as yet undocumented, source of ferret mortality. Finally, recreational shooting of prairie dogs contributes to the problem of lead accumulation in wildlife food chains that include prairie dogs (Knowles and Vosburgh 2001, Pauli and Buskirk 2007, McTee et al. 2019). Killing large numbers of animals, not removing carcasses from the field, and using expanding bullets containing lead may present potentially dangerous amounts of lead to scavengers and predators of prairie dogs. Although no negative effects from ingesting lead have been reported in black-footed ferrets, the cumulative effects of recreational prairie dog shooting along with other stressors can negatively affect black-footed ferret populations.

Prairie dog populations can recover from very low numbers over time following intensive shooting (Knowles 1988, Vosburgh 1996, Dullum et al. 2005, Pauli 2005). It appears that a typical scenario is either: (1) once populations have been reduced, shooters go elsewhere and populations recover; or (2) continued shooting maintains reduced population size at specific sites (Knowles 1988, Vosburgh 1996, Dullum et al. 2005, Pauli 2005). Some landowners charge a fee for recreational shooting and such monetary gain may motivate other landowners to preserve prairie dog colonies for future shooting opportunities (Vosburgh and Irby 1998, Reeve and Vosburgh 2006).

Summary of Effects on the 3Rs

Recreational shooting is a relatively low magnitude but persistent stressor to black-footed ferret populations, especially when it is combined with other stressors such as drought and sylvatic plague (Biggins and Eads 2019). This characterization is a broad evaluation across various types of prairie dog habitat and different prairie dog species. On white-tailed and Gunnison's prairie dog ferret reintroduction sites it may not be a stressor due to relatively low shooting intensities (Reeve and Vosburgh 2006), while on black-tailed prairie dog ferret reintroduction sites it can be a significant stressor. Recreational shooting of prairie dogs likely limits the carrying capacity for ferrets at reintroduction sites, and may appreciably reduce survival and reproduction. As such, recreational shooting may decrease black-footed ferret population resiliency in localized situations, particularly at reintroduction sites located in black-tailed prairie dog habitat. If individual prairie dog colonies are extirpated due to the additive effects of high shooting pressure and other stressors such as sylvatic plague and drought, black-footed ferret population redundancy may be reduced if this occurs over a large portion of the species' range. Since the effects of recreational shooting are most pronounced in black-tailed prairie dog colonies, the representation of black-footed ferret populations may be reduced if populations occurring within this habitat type experience reduced resiliency.

Current and Suggested Conservation Measures

Arizona, Colorado and Utah implement prairie dog shooting closures on public lands from April 1 to June 30 (Arizona), March 1 to June 14 (Colorado) and April 1 to June 15 (Utah) (Arizona Game & Fish Department 2019, Colorado Parks and Wildlife 2019, Utah Division of Wildlife Resources 2018, Regulation R657-19-6). These closures provide protection to prairie dog populations during the crucial breeding and whelping periods, and may reduce the demographic effects of shooting on colonies (Reeve and Vosburgh 2006, Seglund and Schnurr 2010). Other jurisdictions have implemented total shooting closures on prairie dog colonies specifically for the purpose of improving black-footed ferret habitat conditions (U.S. Forest Service 2012), and shooting closures are often a prerequisite for incentive programs focused on black-footed ferret recovery on non-federal lands (NRCS 2014). Since prairie dog mortality by unregulated recreational shooting can greatly exceed predation by black-footed ferrets, implementation of shooting closures is thought to increase prey availability for black-footed ferrets, particularly in instances where sylvatic plague also affects prairie dog populations (Reeve and Vosburgh 2006, Biggins and Eads 2019). Managers should avoid the reintroduction of black-footed ferrets in areas with high levels of recreational prairie dog shooting.

3.2.6 Poisoning of Prairie Dogs

Description

Poisoning of prairie dogs is a major factor in the historical declines of prairie dogs and black-footed ferrets (Forrest et al. 1985, Cully 1993, Forrest and Luchsinger 2006). Similar to many of the other stressors affecting ferret populations, poisoning can affect the ferret directly, through inadvertent secondary poisoning of the ferret caused by consumption of poisoned prairie dogs, or indirectly, through the loss of the prairie dog prey base. The historical estimate of prairie dog occupied habitat is approximately 41 million ha (Anderson et al. 1986). Concerns regarding competition for available forage between livestock and prairie dogs led to the development of extensive government sponsored prairie dog poisoning programs early in the 20th century. Organized prairie dog control gained momentum from 1916–1920, when prairie dogs were poisoned on millions of hectares of western rangeland (Bell 1921). Between 1915 and 1965, the total area poisoned across all states occupied by black-tailed prairie dogs exceeded 15 million hectares, with 1.5 million hectares poisoned in 1923 alone (Forrest and Luchsinger 2006). By the 1960s, occupied prairie dog habitat reached a low of approximately 570,000 ha in the United

States (Bureau of Sport Fisheries and Wildlife 1961, Berryman and Johnson 1973), less than 5% of their historic range (Forrest and Luchsinger 2006). The most recent estimate of prairie dog occupied habitat is approximately 1.5 million ha (74 FR 63343, December 3, 2009; 69 FR 64889, November 9, 2004; 73 FR 6660, February 5, 2008), an increase of 250 percent from its low point.

From the late 1800s to the early 1920s, strychnine was the primary poison for prairie dogs (Bell 1921). Between World War II and 1972, Compound 1080 was the preferred poison for prairie dog control (Forrest and Luchsinger 2006). In 1972, Executive Order 11643 prohibited the use of certain toxicants that might cause secondary poisoning on Federal lands or in federally funded programs. This order was revoked by Executive Order 12342 in 1982. However, poisoning prairie dogs with strychnine and Compound 1080 did not resume. Zinc phosphide became the preferred poison for prairie dog control by 1976, and its use continues to the present (Hanson 1993, Forrest and Luchsinger 2006). In recent years, manufacturers have promoted the use of the anticoagulant rodenticides chlorophacinone (Rozol®) and diphacinone (Kaput®) for control of prairie dogs (Bruening 2007, Lee and Hygnstrom 2007). These chemicals pose a much greater risk than zinc phosphide of secondary poisoning to non-target wildlife that prey upon prairie dogs, such as the black-footed ferret (Erickson and Urban 2004, Vyas et al. 2012).

In May 2009, the U.S. Environmental Protection Agency (EPA) authorized the use of Rozol® throughout much of the range of the black-tailed prairie dog via a Federal Insecticide, Fungicide, and Rodenticide Act Section 3 registration. Rozol® and Kaput-D® are only labeled for the control of black-tailed prairie dogs, and the labels do not allow its use in Arizona or the taking of "endangered species." Furthermore, the EPA has established additional restrictions through the Endangered Species Protection Bulletins that ban the use of Rozol® in black-footed ferret recovery sites. These bulletins are considered an extension of the pesticide label, and it is a violation of federal and state law to use a pesticide in a manner inconsistent with the label.

Despite these regulations, poisoning on or adjacent to black-footed ferret recovery sites is still a concern. The legal use of Rozol® occurs regularly adjacent to one reintroduction site (Butte Creek Ranches, Kansas), and its illegal use occurred at another reintroduction site (Rosebud Reservation, South Dakota) (USFWS 2013a). It is not known if any ferret mortalities directly attributable to Rozol® use occurred at these sites. The ability to verify effects on non-target species such as the ferret is quite limited due to the fossorial nature of ferrets, vegetative cover, possible consumption of poisoned ferrets by other predators, and delayed action of the rodenticide. Only a very small percentage of animals that die from secondary poisoning are ever located. However, the loss of prairie dog occupied habitat that resulted from these poisoning activities reduced the quality and quantity of habitat available to support ferrets. The Service recommended that the EPA withdraw its registration for Rozol® and not issue a registration for Kaput® (Gober 2006, Slack 2006, Arroyo 2009). The Western Association of Fish and Wildlife

Agencies similarly requested that EPA reconsider use of anticoagulants for prairie dog control (Koch 2008). However, Rozol® and Kaput® use to control black-tailed prairie dogs is now legal in most of the western United States.

With the historical decline in prairie dogs, there was a concurrent decline in black-footed ferrets. Poisoning, if thorough enough, may result in permanent loss of prairie dogs, such as occurred in the extirpation of black-tailed prairie dogs in Arizona (Hoffmeister 1986, Arizona Game and Fish Department 1988). This loss can preclude ferret recovery opportunities. More typically, prairie dog numbers are reduced temporarily, but long enough for ferrets to disappear. Efforts to reintroduce prairie dogs, such as with the black-tailed prairie dog in southern Arizona in 2008 (Hale et al. 2013), offer opportunities to create or recreate lost habitat for ferrets.

Prairie dog control to address boundary encroachment issues from expanding prairie dog acreage at the Conata Basin-Badlands black-footed ferret reintroduction site in South Dakota began in 2004 and peaked in 2006, with a 94 percent reduction in toxicant use by 2009 (Griebel 2010). The U.S. Forest Service, in response to local concerns about the effects of drought and prairie dogs, suggested a need to poison prairie dogs in interior portions of the ferret reintroduction area at Conata Basin-Badlands in order to reduce alleged prairie dog damage to native grasslands and balance multiple use needs (U.S. Forest Service 2008). Proposed poisoning in the interior of the site could significantly reduce the viability of this ferret recovery site, as well as reducing the number of wild-born kits available for translocation to other recovery sites. However, the decision whether to allow expanded toxicant use on prairie dog colonies in the interior portion of Conata Basin-Badlands was deferred due to plague epizootics that significantly reduced occupied prairie dog habitat (USFWS 2013a).

Summary of Effects on the 3Rs

Long-term poisoning of prairie dogs can create increase colony fragmentation and reduce overall abundance, causing increased susceptibility to stochastic events and low levels of population resiliency. As an obligate predator of prairie dogs, black-footed ferrets cannot readily adapt to such situations by switching prey resources, and their populations exhibit low abundance, juvenile survival, and resiliency as a result. Extirpation or increased fragmentation of prairie dog colonies reduces black-footed ferret redundancy, as individual ferret populations are extirpated due to reduced prey availability and connectivity between populations. If poisoning is widespread, this can lead to the extirpation of black-footed ferret populations across a variety of ecological settings, reducing genetic variability and resulting in a reduction of the species' representation. However, unlike historic times, poisoning of prairie dogs today largely occurs at local scales without the goal of widespread eradication, and does not result in species-level effects (Forrest and Luchsinger 2006, Seglund et al. 2006). Still, the use of anticoagulant rodenticides remains a localized concern due to secondary poisoning effects. Such effects can occur even if anticoagulants are applied to prairie dog colonies adjacent to black-footed ferret reintroduction sites, resulting in a potential erosion of ferret population resiliency due to edge effects. Black-footed ferret males may be particularly susceptible to these effects due to their larger home ranges relative to females.

Current and Suggested Conservation Measures
Rodenticides such as zinc phosphide are routinely used to control prairie dogs adjacent to black-footed ferret reintroduction sites, which can increase overall social tolerance of prairie dogs and black-footed ferret reintroduction efforts (Griebel 2010, USFWS 2013b). Prohibitions on the use of rodenticides are often a prerequisite for incentive programs focused on black-footed ferret recovery on non-federal lands (NRCS 2014). Zinc phosphide has fewer secondary poisoning effects than anticoagulants (Erickson and Urban 2004), and its use is often prioritized over the use of anticoagulants in black-footed ferret reintroduction areas for this reason. Anticoagulants remain an issue of conservation concern for black-footed ferret populations (USFWS 2013a, Vyas 2013). Regardless of mode of action, rodenticide use and its resultant prairie dog mortality can exacerbate the effects of sylvatic plague, as plague transmission rates can increase as infected fleas accumulate on surviving hosts (Biggins and Eads 2019).

3.2.7 Range Management

Description
Herbivory has always been a component of both the shortgrass prairie and sagebrush-steppe regions of the western United States, and prairie dogs co-evolved with native herbivores such as bison (*Bison bison*), pronghorn (*Antilocapra americana*), and mule deer (*Odocoileus hemionus*) (Osborne 1953, Koford 1958, Miller et al. 1994). In addition to native herbivores, domestic livestock grazing with the historic range of the black-footed ferret began with the arrival of European settlers in the 1800s. The effects of grazing on rangelands are influenced by stocking rate, livestock species, timing and periodicity, and other factors such as drought and fire (Vallentine 1990, Fleischner 1994).

In addition to herbivory, fire historically served as an important disturbance within prairie dog habitat, particularly within black-tailed prairie dog habitat (Augustine et al. 2007). Strong feedback effects can occur between fire and herbivory, affecting both herbivores and the plant communities on which they depend (Coppock and Detling 1986, Coppedge and Shaw 1998). The interaction between fire and herbivory was an important factor in determining the range and extent of black-tailed prairie dog populations (Uresk and Bjugstad 1983), and to a lesser extent determined distribution of white-tailed and Gunnison’s prairie dogs (Baker 2006). Fire typically does not directly affect fossorial animals such as prairie dogs and black-footed ferrets (Lyon et al. 1978), but rather its effects on the vegetative community in turn affect prairie dog population dynamics.

The synergistic effects of disturbances such as herbivory and fire can have positive or negative effects on prairie dog populations, and by extension black-footed ferret populations (Fleischner 1994). For the purposes of this report, we define appropriate range management as actions that positively alter plant community composition in a way that increases the quality of prairie dog habitat. In contrast, poor range management degrades prairie dog habitat and occurs when disturbances are of a magnitude and frequency that prevents the recovery of forage plants (Vallentine 1990).

Within the black-tailed prairie dog portion of the black-footed ferret's historic range, both grazing management and fire can significantly influence vegetative community composition, and thus population resiliency of prairie dogs. Depending on precipitation and site characteristics, black-tailed prairie dogs can compete directly with domestic livestock for forage, resulting in social conflicts (Lamb and Cline 2003), and range degradation if utilization levels are not managed appropriately (Koford 1958, Uresk and Paulson 1988). The degree and severity of competition for forage between black-tailed prairie dogs and domestic livestock is extremely complex, and results have been conflicting or inconclusive (O'Melia et al. 1982, Vermeire et al. 2004, Augustine and Springer 2013, Connell et al. 2019). Regardless of the source of herbivory, overutilization of rangeland decreases habitat quality for black-tailed prairie dogs by reducing the quality and quantity of forage, resulting in lower prairie dog densities and often larger colony sizes as prairie dog territories expand as a result of forage shortages (Facka et al. 2010, Augustine and Springer 2013). This decrease in habitat quality is very similar to the effects of drought, and can result in similar demographic effects for both prairie dogs and black-footed ferrets (see **Section 3.2.2**, above). Under certain conditions, grazing can improve habitat for black-tailed prairie dogs by improving forage quality (Miller et al. 2007, Chipault and Detling 2013, Connell et al. 2019) and facilitating predator detection by reducing vegetative height (Uresk et al. 1981, Cable and Timm 1987).

The effects of range management practices on white-tailed and Gunnison's prairie dogs differ somewhat from the effects described above for black-tailed prairie dogs. In particular, fire has played a smaller role in shaping vegetative communities, as it was much less frequent historically (100 to 450 year intervals vs. 1 to 10 year intervals) in the shrub-steppe habitats occupied by these species (Baker 2006, LANDFIRE 2007). In recent years the role of fire has become more important in lower elevation habitats, as its frequency has increased due to the invasion of non-native annual grasses such as cheatgrass (*Bromus tectorum*) (Crawford et al. 2004, Baker 2006). In contrast, fire frequencies have declined in higher elevation habitats, resulting in the expansion of shrubs and trees (Miller and Rose 1999, Crawford et al. 2004, Baker 2006). These processes have degraded habitat quality for white-tailed and Gunnison's prairie dogs (Lupis et al. 2007), particularly when they are accompanied by forage overutilization (Seglund et al. 2006, Lupis et al. 2007). As is the case in black-tailed prairie dog habitat, properly-managed grazing can increase habitat quality for white-tailed and Gunnison's prairie dogs by increasing forage quality (Pauli et al. 2006), and can be used as a management tool to increase the amount of open habitat preferred by white-tailed prairie dogs (Seglund and Schnurr 2010).

Summary of Effects on the 3Rs

Range management practices that reduce forage quantity and quality decrease prairie dog abundance, fecundity, and juvenile survival (Facka et al. 2010), which in turn makes dependent black-footed ferret populations less resilient. While these practices do not presently occur throughout the potential range of the black-footed ferret, in localized instances the redundancy of black-footed ferret populations can be reduced through loss of connectivity, since black-footed ferrets experience increased mortality when dispersing through unsuitable habitats. This phenomenon is exacerbated by stochastic events such as sylvatic plague and drought. Black-footed ferret representation is reduced if these practices take place across a variety of habitats, resulting in lower genetic variability and ecological diversity. Conversely, the implementation of appropriate range management practices enhances black-footed ferret resiliency, redundancy, and representation if prairie dog habitat quality increases as a result (Augustine and Springer 2013).

Current and Suggested Conservation Measures

Range management practices can be utilized to either maintain or improve prairie dog habitat, and by extension black-footed ferret habitat. Proper allocation of available forage resources between potentially competing herbivores can maintain vegetative communities conducive to prairie dog population resiliency, and application of tools such as prescribed fire can remove visual barriers that hinder prairie dog colony expansion (Seglund and Schnurr 2010, Augustine and Springer 2013). Range management practices that encourage a shifting mosaic of heavily grazed and lightly grazed areas to mimic the historical movement of prairie dog colonies across the landscape (Ernst 2001, Fuhlendorf and Engle 2004) can increase habitat quality for black-footed ferrets while maintaining domestic livestock production levels. Range management practices that favor prairie dog reproduction and colony maintenance can also improve black-footed ferret habitat by providing a reliable supply of prairie dog pups for black-footed ferrets (Biggins et al. 2019 in preparation).

3.2.8 Urbanization

Description

Urbanization represents a permanent loss of potential black-footed ferret habitat, and can entail the direct eradication of prairie dog prey (Hoogland 2006, Lupis et al. 2007, Seglund and Schnurr 2006). Additionally, urbanization fragments and isolates prairie dog colonies, leading to smaller colonies with higher prairie dog densities (Johnson and Collinge 2004). Approximately

1.3 million ha of historical black-footed ferret habitat have been lost to urbanization (Ernst 2001), which is approximately 0.56% of the species' potential range.

While the habitat area required by a population of 30 adult black-footed ferrets (the minimum population size counting toward currently defined recovery goals; USFWS 2013a) is relatively large (≥1,800 ha in black-tailed prairie dog habitats and ≥3,000 ha in white-tailed and Gunnison's prairie dog habitats) and in most cases is not available in urban settings, notable exceptions do occur. In 2015, black-footed ferrets were reintroduced to Rocky Mountain Arsenal National Wildlife Refuge, an undeveloped 5,059 ha tract located on the east side of Denver, Colorado. Despite the presence of single-family homes and other urban development immediately adjacent to the refuge, black-footed ferrets have successfully colonized the refuge, with approximately 29 breeding adults occurring at the site on approximately 1,394 ha of high-density black-tailed prairie dog habitat (USFWS 2018b). Vehicle collisions have been a source of mortality for the ferret population, with six known mortalities reported since the site's initiation in 2015 (N. Kaczor, USFWS, personal communication). Other municipalities have expressed interest in establishing black-footed ferret populations adjacent to urban areas (Boulder County Parks and Open Space 2016). While these observations indicate that urban prairie dog colonies can provide habitat for black-footed ferrets in some instances, prairie dog populations in such colonies are subject to population loss as the degree of fragmentation increases (Magle and Crooks 2009).

Given the significant development pressures in areas such as the Front Range of Colorado, the potential exists for continued loss of potential habitat for black-footed ferrets (74 FR 63343, December 3, 2009). However, it appears that sufficient prairie habitat still occurs within the ferret's historical range to accommodate increases in prairie dog occupied habitat when the 1.3 million ha of urban lands are contrasted with the 163 million ha of current rangeland available within the black-footed ferret's potential range (USFWS 2013a). Similar to the discussion above on the stressor of agricultural land conversion (see **Section 3.2.3**), we recognize that urbanization may affect some prairie dog populations locally, which may impair their ability to potentially serve as black-footed ferret reintroduction sites.

Summary of Effects on the 3Rs

Prairie dog populations subject to the pressures of urban development may become small, isolated, and resource limited. This makes them less resilient and more vulnerable to stochastic events such as plague epizootics and extreme weather events. Decreased connectivity between colonies reduces the ability of migrants to recolonize extirpated colonies, leading to a reduction in redundancy. Given their need for large prairie dog complexes capable of supporting self-sustaining populations in the long term, black-footed ferrets are unlikely to persist in such settings unless the complexes are of sufficient size (see above) and are not subject to further development pressures. However, as discussed above, urbanization is currently affecting only local areas, and sufficient areas of rangeland within the black-footed ferret's potential range remain.

Current and Suggested Conservation Measures
We are not aware of any conservation measures that address the loss of habitat due to urbanization, as this type of habitat conversion is usually permanent in nature. However, if prairie dog complexes large enough to serve as black-footed ferret reintroduction sites are maintained as open space, habitat can be provided for the species in urban settings.

3.2.9 Energy Development

Description
Oil and gas exploration and development as well as alternative energy development (primarily wind and solar) occur throughout the potential range of the black-footed ferret. Between 2004 and 2008, political and economic incentives increased the exploration of oil and gas resources in the Great Plains and intermountain west. The 2005 Energy Policy Act expedited the leasing and permitting of energy development on Federal lands (42 U.S.C. 13201 *et seq*.; Seglund and Schnurr 2010). U. S. energy consumption is expected to increase only slightly in the next 35 years (U. S. Energy Information Administration (EIA) 2019). However, domestic energy production is expected to greatly increase during that same time period with an emphasis on natural gas (EIA 2019). Significant oil and gas development within the black-footed ferret's potential range is expected to continue in Colorado (Seglund and Schnurr 2010), Montana (L. Hanauska-Brown, Montana Fish, Wildlife, and Parks pers. comm.), North Dakota (EIA 2019), Utah (Hersey et al. 2016), and Wyoming (Pocewicz et al. 2014). Alternative energy sources, such as wind and solar, are developing at a rapid pace in Colorado (Seglund and Schnurr 2010) and Wyoming (Pocewicz et al. 2014).

Oil and gas development includes exploration, drilling, production, and site abandonment phases (EPA 2000), each of which may potentially affect the black-footed ferret or its habitat. Seismic methods used for exploration include shot-hole surveys and vibroseis, which is the use of a truck-mounted vibrating plate that sends shock waves through the ground to locate oil sources. These exploration techniques have the potential to result in prairie dog mortality and to crush vegetation along the seismic route (Seglund et al. 2006). However, a study in Wyoming found no correlations between vibroseis activity and burrow collapse or white-tailed prairie dog declines (Menkens and Anderson 1985). Once an oil or gas source is discovered, permanent structures including access roads, well pads, pipelines and any other necessary infrastructure are constructed (EPA 2000). Wells may be in the production phase for up to 20 to 30 years for gas wells (EPA 2000) and up to 100 years for oil wells (Connelly et al. 2004). Although requirements vary by jurisdiction, after production ceases lessees are typically responsible for reclaiming the land back to its original condition, or as close to the original condition as possible (BLM 2007, Sedivec and Saxowsky 2015).

Exploration for oil and gas may increase human activity within previously undisturbed habitats (Underwood 2007). The development of well pads and supporting infrastructure, such as roads and pipelines, reduces and fragments habitat, compacts soil, and destroys vegetation. This infrastructure also creates perches for raptors, which may increase predation pressure on prairie dog colonies near these structures (Pauli et al. 2006). New roads may increase road mortality, and prairie dog shooting may increase with increased human access (Gordon et al. 2003).

The amount of direct habitat loss and total fragmentation associated with oil and gas development varies greatly depending on well density (number of hectares per well) and spacing (distance between individual well pads). Well densities and spacing are typically designed to maximize recovery of the resource and are administered by state oil and gas agencies and the BLM on federal mineral estate. Each geologic basin has a standard spacing, but exemptions are granted (Connelly et al. 2004). Within the potential range of the black-footed ferret, well spacing can vary from 2 to 65 ha per well. Increasing wells per unit area decreases the amount of habitat available for wildlife. Increasing the number of wells per pad increases the size of the individual pad, but also decreases the amount of habitat fragmented. Directional, or horizontal, drilling also decreases the amount of habitat fragmentation by co-locating multiple wells on a single pad (Copeland et al. 2009). On BLM lands in Wyoming, single drill pads average 1.2 ha, but this estimate varies widely between projects (BLM 2007). Variation in well pad size and spacing results in variation of the intensity of effects from energy development across the potential range of the black-footed ferret. The threshold levels of oil and gas development that result in population-level effects to the black-footed ferret are unknown.

For our analysis of oil and gas development within the black-footed ferret's potential range, we applied a 1.37 ha pad scar footprint on all known producing and non-producing wells within the species' range, following the methods of Garman and McBeth (2014). This footprint more accurately describes the spatial effect of a well, rather than just the point of the well itself, because it attempts to account for the infrastructure and vegetation disturbance associated with well development. Although one may assume the amount of disturbance is less for a non-producing well than a producing well, we included them in our analysis because we cannot estimate the level of post-production restoration that has occurred on-site. Restoration of a closed well pad site to its natural condition may take up to 40 to 50 years (S. Garman, USGS, pers. comm.). Within the black-footed ferret's potential range, 429,491 ha are affected by producing and non-producing well footprints, corresponding to 0.19 percent of the species' potential range (Figure 6).

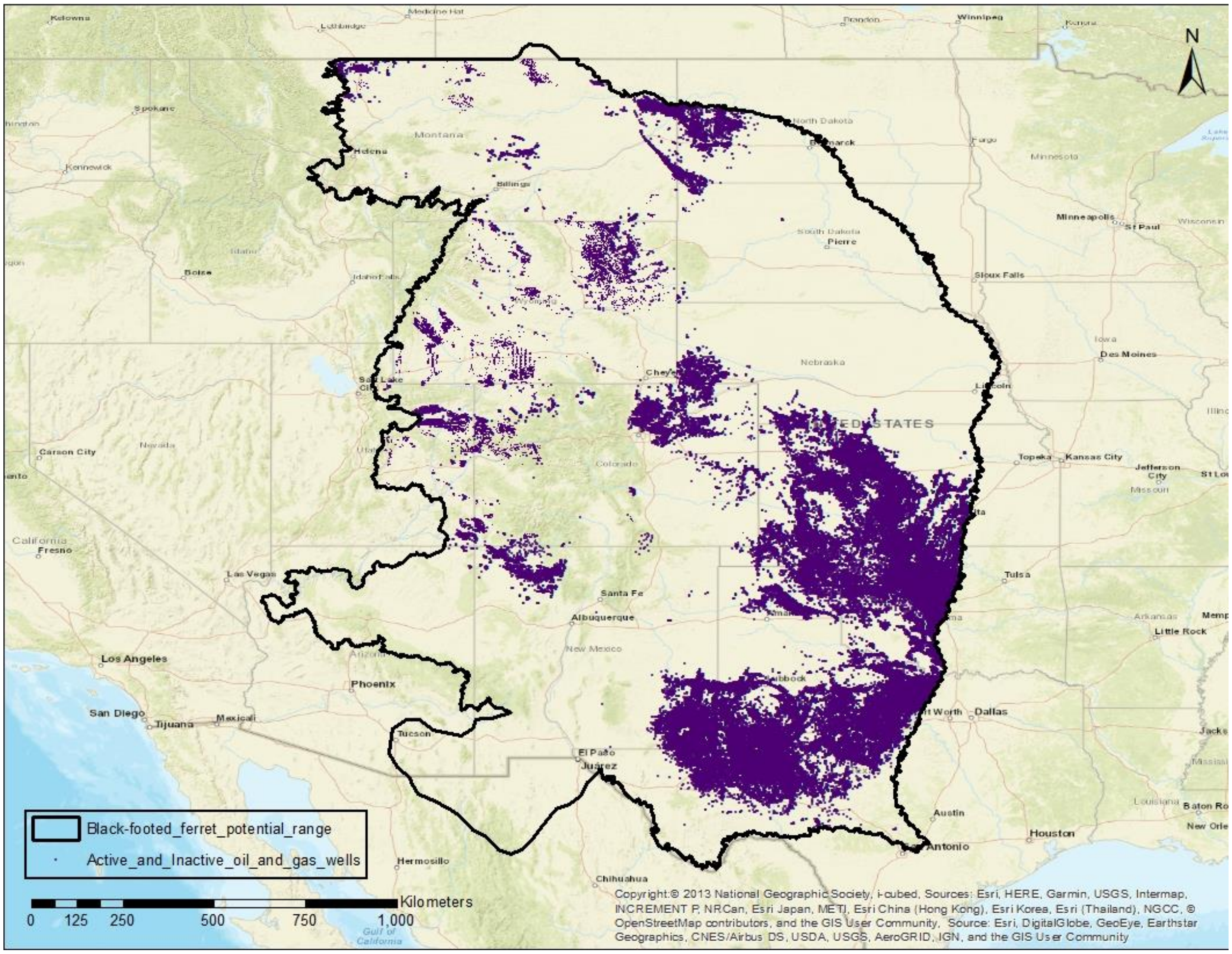

Figure 6. Map showing active (producing) and inactive (non-producing) oil and gas wells located in the potential range of the black-footed ferret. Footprints of oil and gas wells comprise 0.19 percent of the black-footed ferret's potential range. Because of the scale of this map, the points representing oil and gas wells overestimate the true area of the well footprints, making it appear to be greater than 0.19 percent of the potential range. The footprints are displayed in this manner so the reader is better able to see concentrations of oil and gas development with the potential range of the black-footed ferret. Spatial data from IHS Markit (2019).

Like oil and gas development, wind energy development can affect black-footed ferret habitat during the construction and operation phases, and projects result in some permanent loss of habitat. On a per-megawatt basis, wind energy has a larger footprint than most forms of energy (Kiesecker et al. 2011). In an analysis of 172 existing and proposed wind energy development projects, Denholm et al. (2009) estimated direct area affected due to permanent disturbances such as roads, turbine pads, and substations, as well as the total area encompassed by the footprint of each wind project. Although estimates of total area varied widely due to differences in wind plant configuration, Denholm et al. (2009) estimated an average area requirement of 0.3 ha per MW of installed wind energy for direct area affected, and an average of 34.5 ha per MW for the total area affected. We used the USGS U.S. Wind Energy Turbine Database (Hoen et al. 2019) to determine the installed wind energy capacity within the potential range of the black-footed ferret (Figure 7). Based on these data, there is 41,608 MW of installed wind energy in the potential range, with a direct effect of 12,482 ha and a total area affected footprint of 1,435,476 ha. These estimates comprise 0.005 percent and 0.62 percent of the potential range of the black-footed ferret, respectively. While this is a small portion of the black-footed ferret's potential range and some potential habitat is likely available within the total area of a wind plant footprint, projects can potentially have significant local effects. For example, a planned wind energy development in Shirley Basin, Wyoming is located in the center of a black-footed ferret reintroduction site, and managers are closely monitoring prairie dog and ferret abundance in the area to evaluate potential impacts (Wyoming Game and Fish Department 2018). Roads and transmission line corridors associated with wind energy developments may also increase predation on ferrets by generalist predators such as coyotes (*Canis latrans*) (Forman et al. 2003).

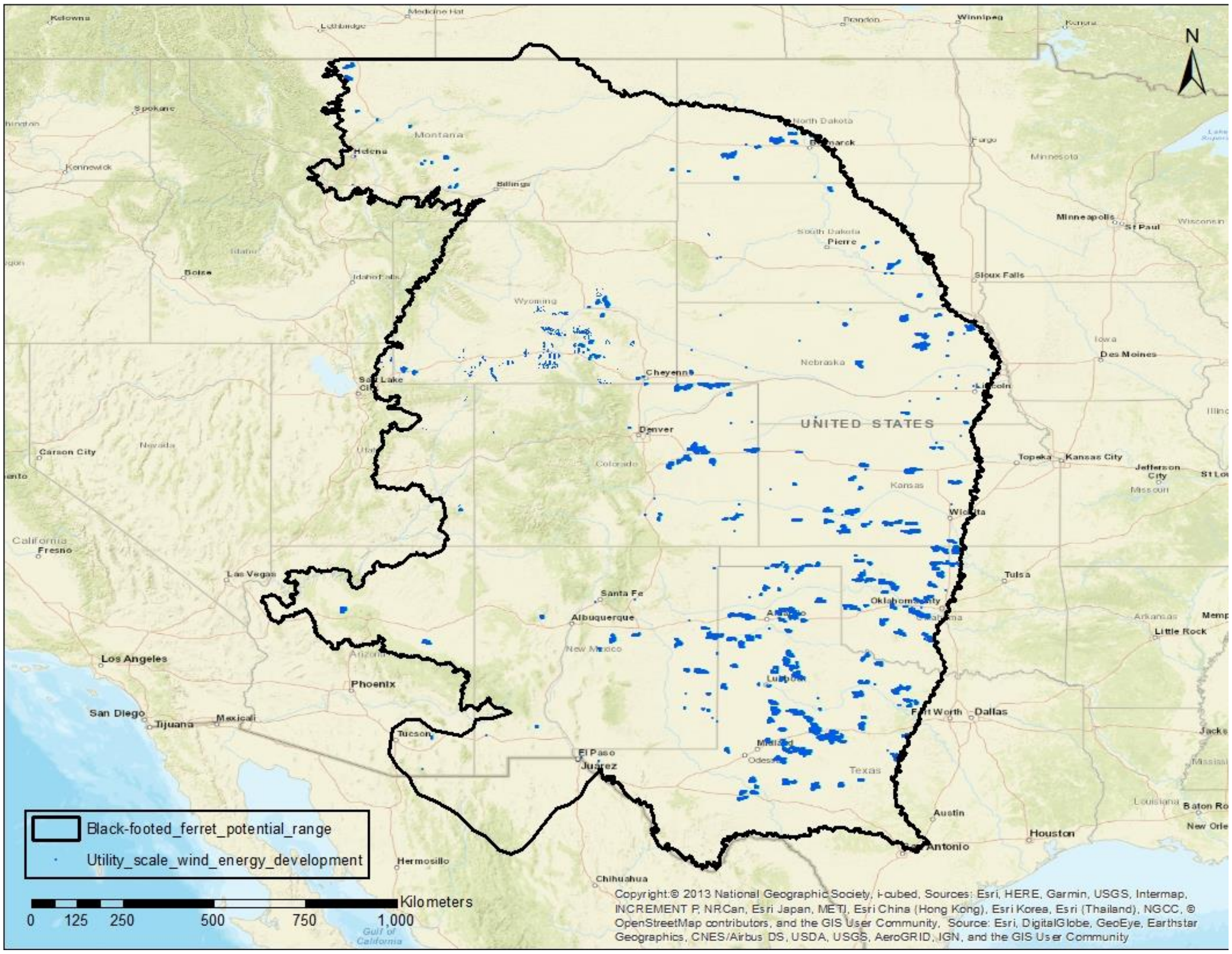

Figure 7. Map showing utility scale (> 100 kilowatts) wind energy development projects located in the potential range of the black-footed ferret. Direct loss of habitat due to placement of permanent structures comprises 0.005 percent of the black-footed ferret's potential range, and the total summed footprints of each wind project comprise 0.62 percent of the range. Because of the scale of this map, the points representing individual wind turbines overestimate the true area of each project, making it appear to be greater than 0.62 percent of the potential range. The footprints are displayed in this manner so the reader is better able to see concentrations of wind energy development with the potential range of the black-footed ferret.

Utility scale solar energy developments also occur within the potential range of the black-footed ferret, but comprise a much smaller portion of the potential range than other forms of energy development. The Solar Projects Database (Solar Energy Industries Association 2019) lists 11 utility scale (10 MW or greater) project within the potential range, with an average footprint of 3.7 ha/MW. While utility scale solar projects can alter potential black-footed ferret habitat permanently, at present they occupy a negligible portion of the species' potential range.

Summary of Effects on the 3Rs

Reduction in habitat quality and quantity due to energy development could make prairie dog populations less resilient, and preclude their availability as potential black-footed ferret habitat. Fragmentation of occupied habitat can reduce the ability of black-footed ferrets to disperse to new habitats, through either direct mortality or a reduction in gene flow and genetic fitness, leading to a reduction in population resiliency and redundancy. However, energy development represents a very small portion of the total black-footed ferret potential range, and as such does not preclude the establishment of additional reintroduction sites in most instances.

According to our analysis, energy development currently affects less than one percent of the black-footed ferret's potential range. While we recognize that energy development can have localized effects at some black-footed ferret reintroduction sites, it does not appear to be a major factor influencing the resilience of the species at this time.

Current and Suggested Conservation Measures

Conservation efforts focused on white-tailed prairie dog and Greater sage-grouse conservation in the state of Wyoming may have beneficial effects for black-footed ferrets. In 2007 the Bureau of Land Management (BLM) issued a Statewide Programmatic White-tailed Prairie Dog Biological Evaluation that recommended several conservation practices to minimize effects to white-tailed prairie habitat (BLM 2007). These practices included locating new access roads away from existing colonies, prohibiting development in occupied colonies, including conditions in oil and gas drilling permits to protect prairie dogs during the breeding season (April 1 – July 15), and encouraging the use of directional drilling. Many of these practices have also been included in Resource Management Plans (RMP) for BLM field offices throughout the range of the white-tailed prairie dog, which includes several existing and potential black-footed ferret reintroduction sites (Luce 2006).

Several restrictions on energy development in Greater sage-grouse habitat in Colorado, Utah, and Wyoming may also benefit white-tailed prairie dogs, and create or maintain black-footed ferret reintroduction sites. These restrictions include co-locating disturbance activities, prohibition of permanent surface occupancy in identified core areas, seasonal restrictions on production activities, and prohibitions on wind energy development in core areas (BLM 2019, State of Wyoming Executive Order 2015-4). Since white-tailed prairie dog habitat overlaps with Greater sage-grouse habitat in these states (Mack et al. 2017), habitat quality may be enhanced for portions of the black-footed ferret potential range as well.

3.3 Historical Condition

3.3.1 Distribution

As indicated in **Section 2.1.2**, the black-footed ferret's historical distribution coincided with the distribution of black-tailed, Gunnison's, and white-tailed prairie dogs (Figure 2). These prairie dog species collectively occupied approximately 41 million ha of intermountain and prairie grasslands extending from Canada into Mexico (Anderson et al. 1986, Biggins et al. 1997). The habitat occupied by prairie dogs existed within a range of an estimated 237 million ha (Ernst 2006). There has been no documented occurrence of the ferret within the range of either the Utah prairie dog or the Mexican prairie dog, whose ranges are small and disjunct (Lockhart et al. 2006). Ferrets from Arizona, Colorado, Kansas, Montana, Nebraska, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, Utah, Wyoming, Alberta, and Saskatchewan have been collected as museum specimens since the late 1800s (Anderson et al. 1986). Ferrets also likely occurred in Mexico in recent times, as evidenced by: (1) the fairly contiguous historical distribution of prairie dogs in Arizona, New Mexico, and Mexico, (2) the similarity of biological communities in these areas, (3) the presence of a museum specimen from a site just north of the Mexico and U.S. border, and (4) fossil records farther south in Mexico (Anderson et al. 1986).

Ernst (2006) utilized a geographic information system database to identify the likely distribution of prairie dog habitat where the black-footed ferret probably occurred historically in the United States. Ernst concluded that 85 percent of all ferrets may have occurred in black-tailed prairie dog habitat, 8 percent in Gunnison's prairie dog habitat, and 7 percent in white-tailed prairie dog habitat. Although potential biases are possible in this characterization of the historical distribution of ferrets, most ferrets probably occurred in black-tailed prairie dog habitat based on the more expansive extent of their distribution.

3.3.2 Abundance

The black-footed ferret's close association with prairie dogs was an important factor in its decline. From the late 1800s to approximately 1960, both prairie dog occupied habitat and prairie dog numbers were reduced by: (1) habitat destruction due to conversion of native prairie to cropland, (2) poisoning, and (3) disease. The ferret population declined precipitously as a result (Lockhart et al. 2006). The ferret was considered extremely rare before a small population was located in Mellette County, South Dakota, in 1964 (Henderson et al. 1969), and no abundance data exist apart from museum specimens (Anderson et al. 1986). Breeding attempts with a few captured animals failed to produce surviving young. The last wild animals in the Mellette population were observed in the field in 1974 (Clark 1989). The last captive animal from the Mellette population died at Patuxent Wildlife Research Center in 1979 (USFWS 1988) and the ferret was presumed extinct.

In 1981, a remnant population was discovered near Meeteetse, Wyoming (Clark et al. 1986, Lockhart et al. 2006). At its peak in 1984, the Meeteetse population numbered 129 animals, with 43 adults and 86 juveniles observed (Forrest et al. 1988). Outbreaks of canine distemper and sylvatic plague occurred at Meeteetse in the early 1980s, and all surviving wild ferrets at Meeteetse were removed during 1985–1987. These ferrets were used to initiate a captive breeding program. Of the 18 remaining ferrets captured from Meeteetse, 15 individuals, representing the genetic equivalent of seven distinct founders, produced a captive population lineage that is the foundation of present recovery efforts (Hutchins et al. 1996, Garelle et al. 2006). Extant populations, both captive and reintroduced, descend from these “founder” animals.

No wild populations of black-footed ferrets have been found following the final capture of the last known Meeteetse ferret in 1987, despite extensive and intensive searches throughout the historic range of the ferret. It is very unlikely that any undiscovered wild populations remain (Hanebury and Biggins 2006, Lockhart et al. 2006).

3.4 Current Condition

3.4.1 Distribution

Black-footed ferrets currently occur in both captive and wild populations, and have been purposefully managed as such since 1987, when the last remaining wild population in Meeteetse, Wyoming was rescued to establish a captive breeding program for the species (Lockhart et al. 2006, USFWS 2013a). The captive black-footed ferret population is guided by the Association of Zoos and Aquariums (AZA) Black-footed Ferret SSP® to conserve a minimum breeding population of 240 ± 35 animals of optimum sex and age ratio to maximize productivity and genetic diversity (Hutchins et al. 1996). Captive ferrets in excess of SSP® needs are allocated each year for reintroduction or for scientific and educational purposes. Animals used for scientific or educational purposes are often older animals that are past prime breeding age, although some kits have also been allocated for research purposes. For example, some ferrets have been used for research and development of a plague vaccine (Rocke et al. 2006). Not including non-reproductive animals housed at zoos and nature centers for outreach purposes, the captive black-footed ferret population numbers 301 animals as of 2018 and is housed at six captive breeding facilities in the United States and Canada (Table 2).

Since the reintroduction of black-footed ferrets into the wild in 1991 at Shirley Basin, Wyoming, captive ferrets in excess of SSP® needs have been reintroduced at 29 reintroduction sites in the western United States, Canada, and Mexico. At present, 14 sites are occupied by ferrets, with the other 15 sites being extirpated due to sylvatic plague. Table 3 provides more detailed characteristics of each reintroduction site as well as its current and past performance.

Table 2. Location and number of breeding age black-footed ferrets housed at captive breeding facilities in the United States and Canada, 2018.

Facility Name	Location	# of male BFF	# of female BFF
National Black-footed Ferret Conservation Center (NBFFCC)	Carr, CO	74	106
Smithsonian Conservation Biology Institute (SCBI)	Front Royal, VA	14	19
Louisville Zoological Garden (LZG)	Louisville, KY	14	15
Cheyenne Mountain Zoo (CMZ)	Colorado Springs, CO	9	13
Phoenix Zoo (PHZ)	Phoenix, AZ	12	16
Toronto Zoo (TOR)	Toronto, ON	3	5
TOTALS		**126**	**175**

Table 3. Black-footed ferret reintroduction site characteristics and current status as of 2018.

Site Name and Location	Year(s) Initiated	PD Species[1]	Active PD Hectares	Potential PD Hectares	Active?	#BFF Fall 2018[2]	Max # Fall BFF seen (Year)[2,3]
Shirley Basin, WY	1991	WTPD	21,711	73,574	Yes	30	229 (2006)[4]
Conata Basin-Badlands, SD	1994, 1996	BTPD	5,494	12,141	Yes	119	355 (2007)
UL Bend NWR, MT	1994	BTPD	202	728	Yes	1	56 (1999)
Aubrey Valley/Double O Ranch, AZ	1996, 2016	GPD	26,485	106,846	Yes	9	123 (2012)
Ft. Belknap Reservation, MT	1997	BTPD	688	3,035	Yes	11	55 (1998)
Coyote Basin, CO/UT	1999	WTPD	10,117	19,830	Yes	3	45 (2003)
Cheyenne River Sioux Tribe, SD	2000	BTPD	2,428	16,592	No	0	173 (2006)
Wolf Creek, CO	2001	WTPD	1,594	12,141	No	0	38 (2001)
BLM 40 Complex, MT	2001	BTPD	202	486	No	0	10 (2004)
Janos, MX	2001	BTPD	2,226	15,000	No	0	15 (2003)
Rosebud Sioux Tribe, SD	2003	BTPD	1,012	28,329	No	0	30 (2004)
Lower Brule Sioux Tribe, SD	2006	BTPD	723	2,226	Yes	10	29 (2010)
Wind Cave NP, SD	2007	BTPD	739	1,133	Yes	18	49 (2010)
Espee Ranch, AZ	2007	GPD	8,811	56,356	No	0	22 (2008)
Butte Creek Ranches, KS	2007	BTPD	2,145	3,157	Yes	13	79 (2011)
Northern Cheyenne Tribe, MT	2008	BTPD	324	3,440	No	0	6 (2009)
Vermejo Park Ranch (BTPD), NM	2008	BTPD	4,047	4,047	No	0	28 (2010)
Grasslands NP, SK	2009	BTPD	769	3,561	No	0	17 (2010)
Vermejo Park Ranch (GPD), NM	2012	GPD	405	1,619	No	0	5 (2013)
Walker Ranch, CO	2013	BTPD	340	1,195	No	0	3 (2014)
City of Fort Collins, CO	2014	BTPD	746	1,619	Yes	8	11 (2016)
North Holly, CO	2014	BTPD	55	1,514	No	0	1 (2015)
Liberty, CO	2014	BTPD	93	607	No	0	2 (2015)
Rocky Mountain Arsenal NWR, CO	2015	BTPD	1,214	1,214	Yes	79	79 (2018)
Crow Reservation, MT	2015	BTPD	1,985	3,316	Yes	10	22 (2017)
South Holly, CO	2015	BTPD	120	689	No	0	1 (2015)
Meeteetse, WY	2016	WTPD	2,236	2,870	Yes	26	129 (1984)
Bad River Ranch, SD	2017	BTPD	121	1,335	No	0	8 (2017)
Moore Ranch, NM	2018	BTPD	164	609	Yes	3	3 (2018)
TOTALS			**97,197**	**379,210**		**340**	**1,623**

[1]WTPD=white-tailed prairie dog, BTPD=black-tailed prairie dog, GPD=Gunnison's prairie dog

[2]Minimum number alive (MNA) unless otherwise noted

[3]Numbers reported do not necessarily correspond with Active or Potential PD acres as reported in this table; area surveyed varies by year at most sites

[4]Correlated density estimate derived from 8,369 ha survey area

3.4.2 Abundance

3.4.2.1. Captive Black-footed Ferret Population

While the total captive black-footed ferret population is kept relatively stable at approximately 280 animals for reasons described above, population performance can be measured on an annual basis by comparing various measures of reproductive performance. In the context of captive breeding, whelping is defined as a female giving birth to one or more kits, either alive or stillborn (USFWS 2017). Whelping success rates for the captive population have declined in recent years (Figure 8).

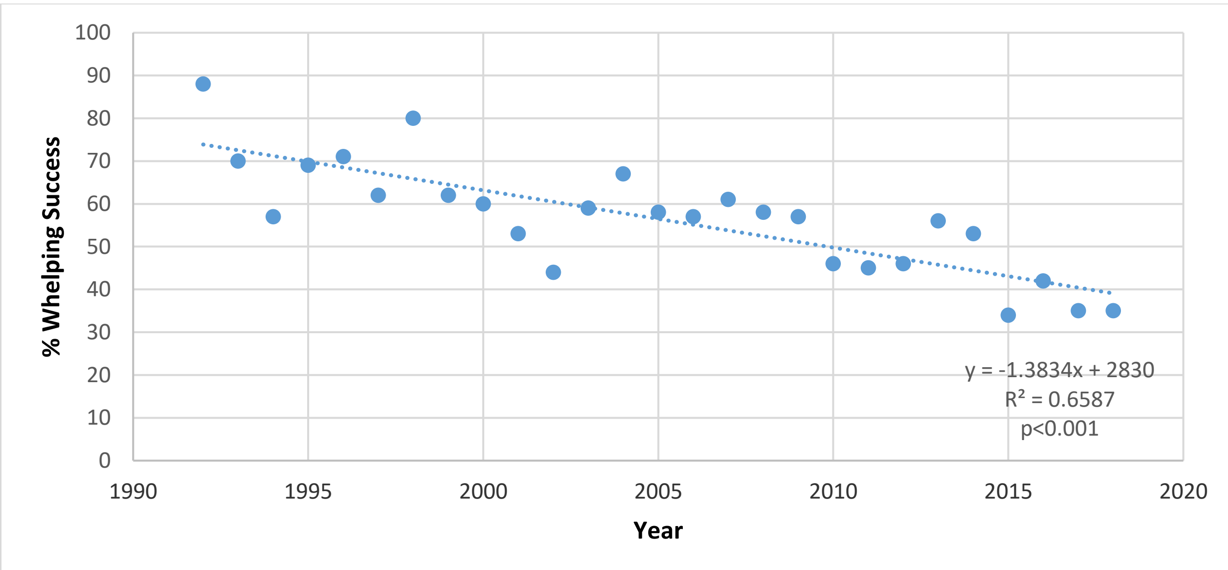

Figure 8. Overall whelping success rates for the captive black-footed ferret population (all facilities), 1992-2018.

Captive black-footed ferret population performance is also measured by the mean number of kits born per litter (Figure 9) and percentage of kits born that are successfully weaned (Figure 10). Unlike whelping rates, these measures have been stable to increasing over the life of the captive breeding program, although kit weaning percentages have declined in recent years. The increase in the mean number of kits born per litter over time may be due to the stability of food resources in the captive setting rather than hereditary factors; this phenomenon has been observed in other species reared in captivity (Jaquish et al. 1996).

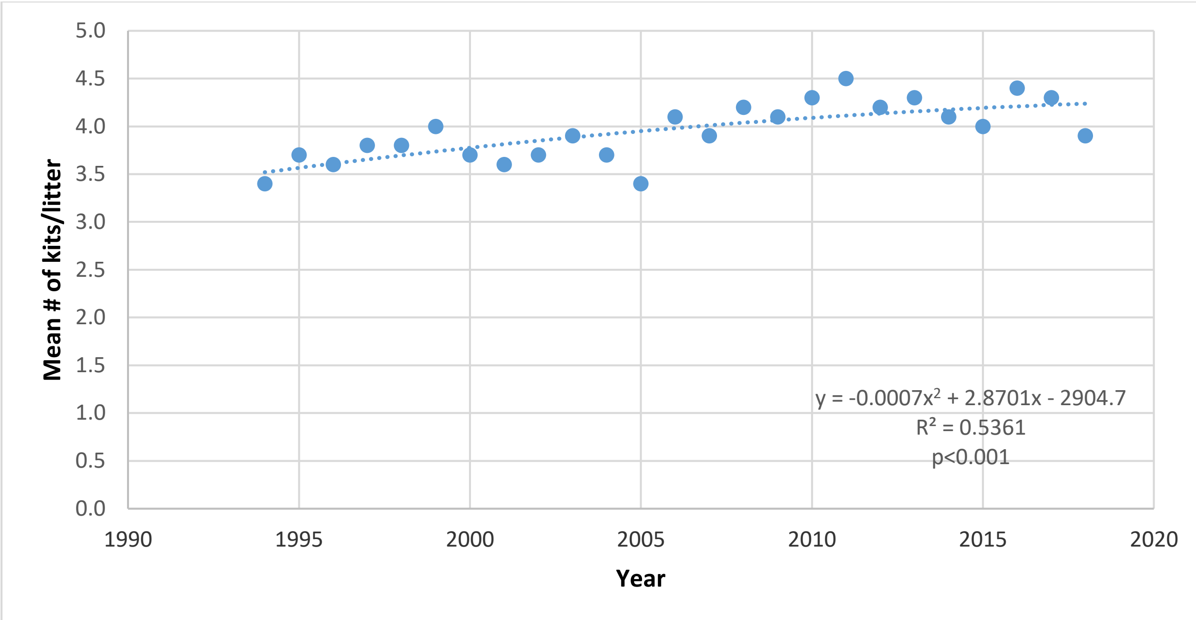

Figure 9. Mean number of kits born per litter for the captive black-footed ferret population (all facilities), 1994-2018.

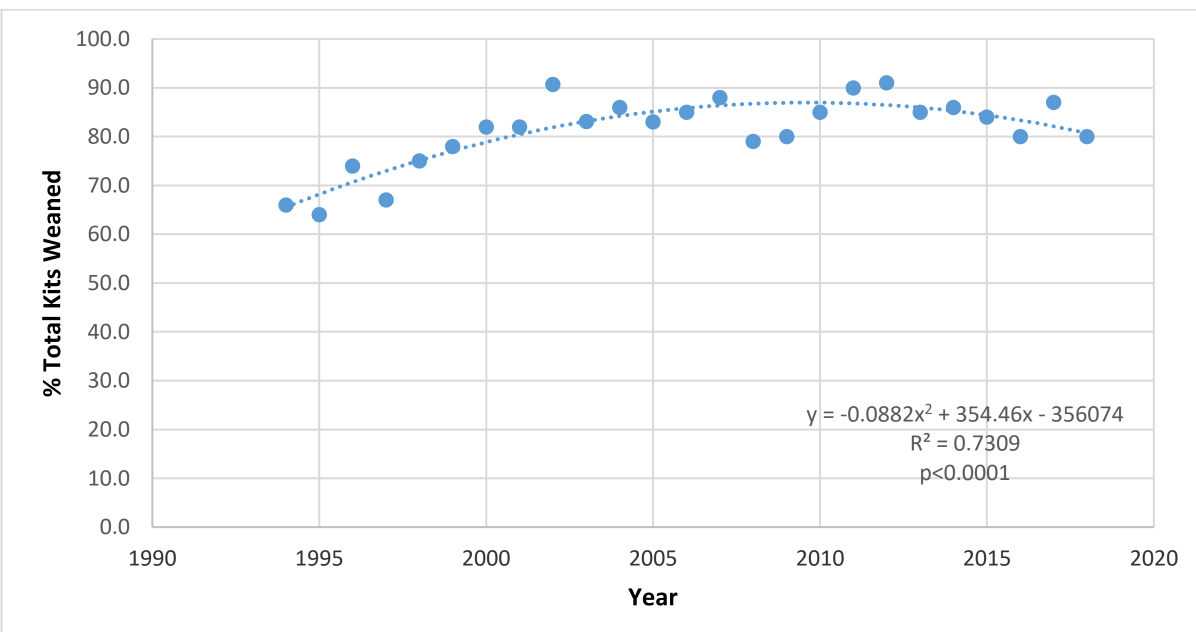

Figure 10. Percentage of total kits born and successfully weaned for the captive black-footed ferret population (all facilities), 1994-2018.

3.4.2.2 Reintroduced Black-footed Ferret Population

Accurate population estimates for the reintroduced black-footed ferret population are difficult to obtain, due to the species' reclusive nature and a lack of available resources (USFWS 2013a), which preclude comprehensive survey efforts at every reintroduction site every year. Reintroduction sites generally obtain population estimates via fall spotlight surveys that attempt to enumerate black-footed ferret adults and young of the year (Biggins et al. 2006b, USFWS 2016a). The population estimates presented herein are likely biased low due to incomplete survey efforts; however, they are useful for comparative purposes, and trend analyses provide an indicator of the relative resiliency of each reintroduction site. Population estimates reported by reintroduction sites are expressed as minimum number alive (MNA; Krebs 1966), which serves as an index of ferret abundance. Although the MNA index does not account for incomplete and variable detectability, it is generally believed to detect >82% of adult ferrets present (Forrest et al. 1988, Biggins et al. 2006b). Based on long-term data from several reintroduction sites, fall MNA data are comprised of approximately 33% adults and 67% young of the year, and overwinter survival data indicate that one-half of the fall MNA estimate is an accurate estimate of spring breeding adults (USFWS 2013a). Data presented in this report come from a variety of sources, most commonly from annual reports issued to the Black-footed Ferret Recovery Implementation Team (BFFRIT) Conservation Subcommittee. Data are available from the Service upon request.

Unlike the captive black-footed ferret population, sites within the reintroduced ferret population are subject to a high degree of year-to-year variability due to drought, sylvatic plague epizootics, and other stochastic events. These fluctuations are apparent when analyzing the overall population trend for the species, which increased steadily from the early 1990s until approximately 2007, after which it began to decline (Figure 11).

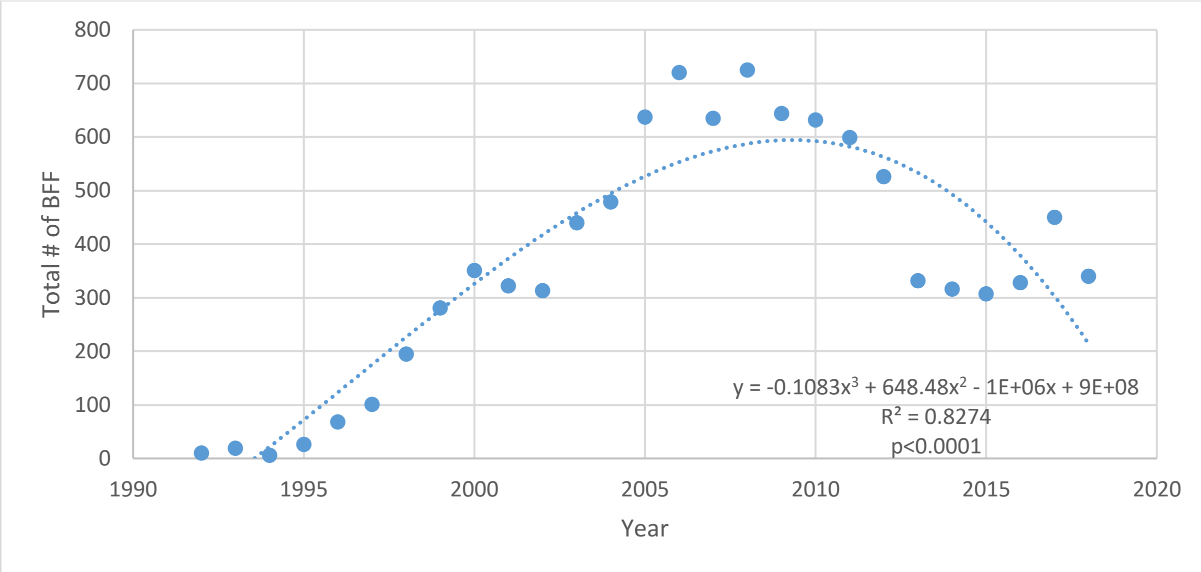

Figure 11. Overall population trend for the reintroduced black-footed ferret population, 1992-2018.

Despite the addition of several new reintroduction sites since the beginning of reintroduction efforts in 1991, population levels for the black-footed ferret reintroduced population have failed to keep pace with the rate at which new sites were developed (Figure 12). The primary reason for this phenomenon (and the extirpation of several reintroduction sites) is the occurrence of sylvatic plague epizootics. Sylvatic plague was not documented in South Dakota until 2006, after which it severely affected the Conata Basin-Badlands and Cheyenne River reintroduction sites, which were two of the largest sites in terms of total number of black-footed ferrets (USFWS 2013a).

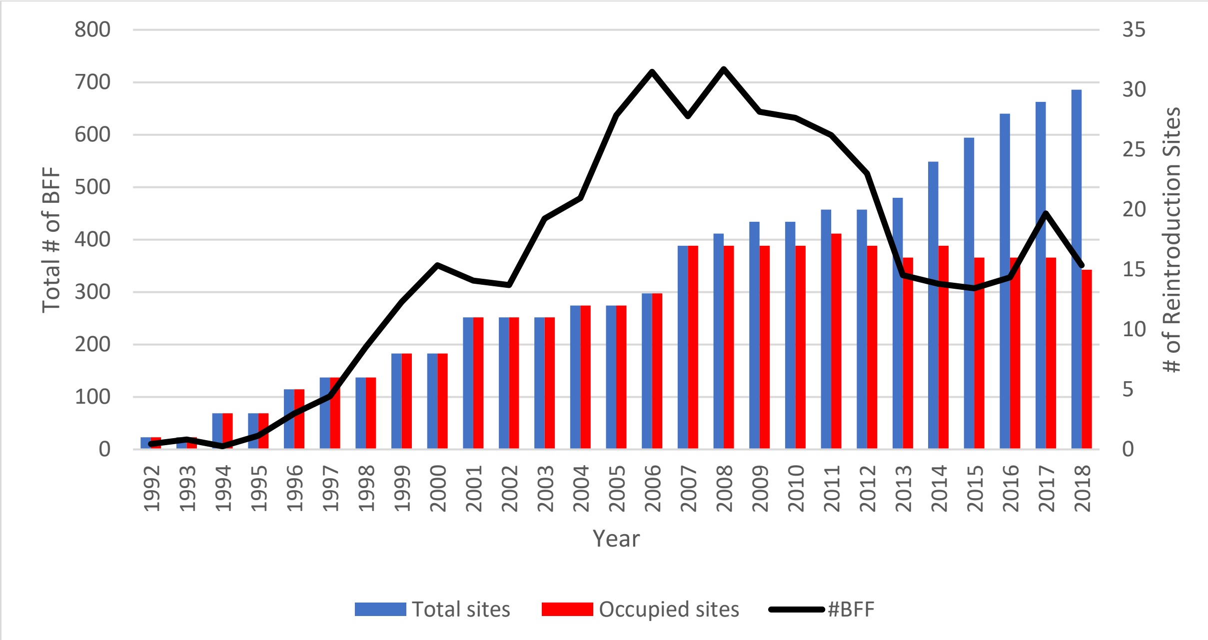

Figure 12. Black-footed ferret population levels and reintroduction site recruitment trends, 1992-2018.

The association between total number of reintroduction sites and black-footed ferret population levels was strongly positive from 1992 to 2007 ($F_{1,14}$=86.42, r^2=0.86, p<0.01), but much less so from 2008 to 2018 ($F_{1,25}$=11.07, r^2=0.31, p<0.01). This divergence noted in 2008 is likely the result of sylvatic plague epizootics at several reintroduction sites, as well as differences in the characteristics of reintroduction sites added during the periods 1992-2007 and 2008-2018. Analysis of variance shows that reintroduction sites added during the latter period are significantly smaller in mean initial size (1,235.3 ha vs. 6,531.6 ha; $F_{1,14}$=8.71, p<0.05) and have fewer mean years of persistence before extirpation (3.4 vs. 8; $F_{1,14}$=9.21, p<0.01).

The size of reintroduction sites, along with the density of prairie dog prey, level of conservation efforts, sylvatic plague, drought, and other abiotic factors, plays a significant role in their ability to support black-footed ferret populations. A breeding population of 30 adults was established as the minimum recovery criterion (USFWS 1988, USFWS 2013a) largely based on population studies conducted at Meeteetse, Wyoming, the last free-ranging population of black-footed ferrets that formed the basis for all subsequent black-footed ferret recovery efforts. Although the Meeteetse population was studied intensively for only a short time (1981-1985), researchers assumed that it had persisted as a geographically isolated population over the long term prior to its discovery in 1981. Researchers also assumed that the observed maximum count of 43 adults and 86 juveniles in the fall of 1985 was representative of the site's potential (Forrest et al. 1985, USFWS 1988).

Considerable debate has occurred over what constitutes a minimum viable population size, and the 30 breeding adult criterion falls below the "50/500 rule" effective population size guideline that is often cited as a management goal for imperiled species (Franklin 1980, Brook et al. 2011). However, for management-intensive species such as the black-footed ferret, frequent intervention in the form of plague management (vector control and/or individual ferret vaccination) and population augmentation is required in order to prevent the extirpation of individual reintroduction sites. This paradigm follows examples cited by Garnett and Zander (2011) and Jamieson and Allendorf (2012), in which extinction risk due to invasive species and other factors is insensitive to effective population size or levels of genetic diversity, and those other factors pose a much more immediate risk of extinction. Self-sustaining black-footed ferret reintroduction sites have been established successfully in recent years, provided plague management and sufficient amounts of suitable habitat are available (Grenier et al. 2007, Jachowski et al. 2011a, USFWS 2018b). These instances suggest that availability of suitable habitat and implementation of appropriate management practices may take precedence over adherence to strict effective population size parameters, although such factors should be carefully considered in the future recovery strategy for the species, particularly in the context of reproductive fitness and evolutionary potential (Traill et al. 2010, Frankham et al. 2014). Modeling efforts have illustrated the roles of minimum population size, carrying capacity, and the need for periodic population augmentation (CBSG 2004), although these efforts have not explicitly accounted for the role of stressors such as sylvatic plague (Figure 13).

Regardless of the utility of the 30 breeding adult criterion as a minimum viable population size, black-footed ferret reintroduction sites have struggled to meet this level, and few can be considered resilient in the context of achieving stated recovery goals in the 2013 Recovery Plan (USFWS 2013a). An analysis of comprehensive survey data from the only five reintroduction sites to ever meet the minimum 30 breeding adult criterion (Aubrey Valley, Arizona; Butte Creek Ranches, Kansas; Cheyenne River Reservation, South Dakota; Conata Basin-Badlands, South Dakota; and Shirley Basin, Wyoming) showed that the amount of habitat needed by each breeding female exceeded parameters established in the 2013 Black-footed Ferret Recovery Plan (USFWS 2013a). The mean observed area per adult female for black-tailed prairie dog habitat (data from Butte Creek Ranches, Cheyenne River, and Conata Basin-Badlands), Gunnison's prairie dog habitat (data from Aubrey Valley), and white-tailed prairie dog habitat (data from Shirley Basin) is shown in Table 4. Figure 14 depicts each reintroduction site's maximum observed size and its projected ability to meet the 30 breeding adult criterion using the mean observed ha/female data from Table 4.

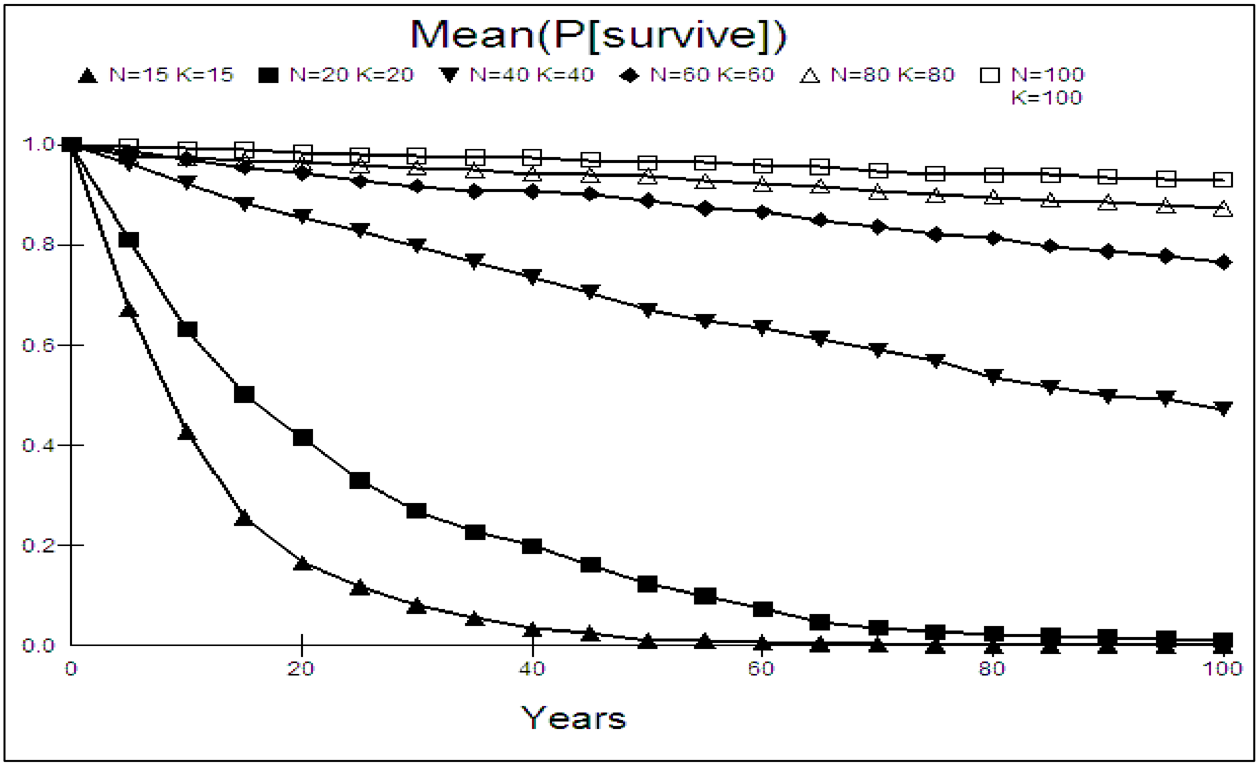

Figure 13. Mean probability of persistence for simulated black-footed ferret populations of different initial size (N), with carrying capacity (K) equal to initial size. From CBSG (2004).

Table 4. Observed area per female (hectares/female) for black-footed ferret reintroduction sites in black-tailed, Gunnison's, and white-tailed prairie dog habitats.

Habitat Type	Mean observed ha/female	95% CI	2013 Recovery Plan ha/female guideline
Black-tailed prairie dog	154.1	±25.7	90.0
Gunnison's prairie dog	649.9	±179.3	152.0
White-tailed prairie dog	227.1	±85.2	152.0

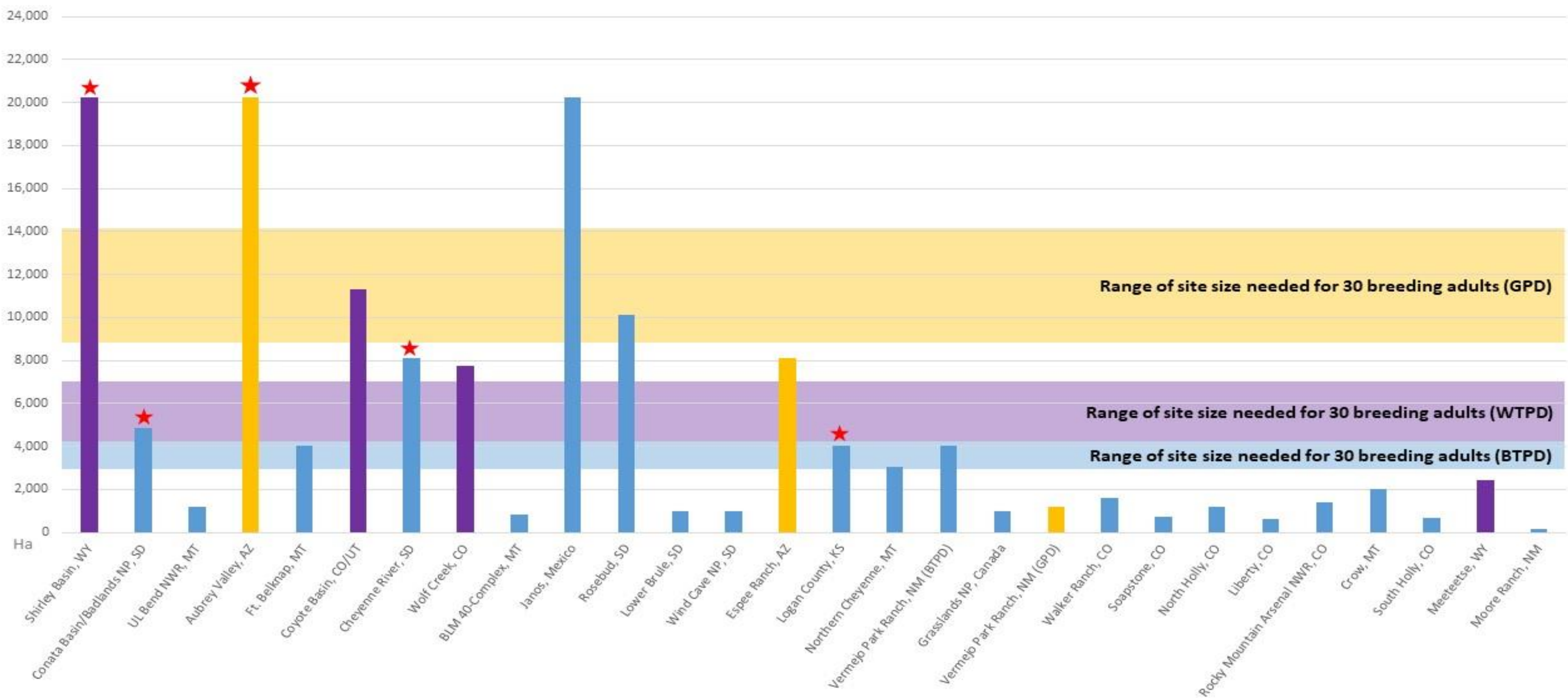

Figure 14. Maximum observed size (ha) of black-footed ferret reintroduction sites and its relationship to confidence intervals showing the range of site sizes needed to support ≥ 30 breeding adult black-footed ferrets in black-tailed (BTPD), Gunnison's (GPD), and white-tailed (WTPD) prairie dog habitats. Sites are displayed chronologically (left to right) in the order they were initiated. Stars above bars denote sites that have reached the ≥ 30 breeding adult criterion at some point in the past.

We acknowledge that the use of observed area per female to determine minimum habitat area requirements for black-footed ferrets can be problematic, since survey efforts typically do not locate all individuals at a reintroduction site. However, the minimum number alive population estimation methodology used at several reintroduction sites accounts for >82% of all individuals present (Forrest et al. 1988, Biggins et al. 2006b), and more intensive survey data are available for some reintroduction sites that help define minimum habitat area requirements. Data from the Rocky Mountain Arsenal National Wildlife Refuge and UL Bend National Wildlife Refuge reintroduction sites (both located in black-tailed prairie dog habitat) constitute black-footed ferret censuses, and these data illustrate the utility of the suggested area per female guideline found in the 2013 Recovery Plan (USFWS 2013a). The observed area per female at Rocky Mountain Arsenal is 89 ha/female (USFWS 2018b), and the observed area per female at UL Bend is 118 ha/female (USFWS 2018c). Rather than being a conservative estimate as described in the 2013 Recovery Plan, the 90 ha/female criterion for ferrets occupying black-tailed prairie dog habitats (USFWS 2013a) may reflect actual breeding female habitat needs. The discrepancy between the 90 ha/female criterion and the earlier 30 ha/female estimate developed by Biggins et al. (1993) may be due to social behavior of female black-footed ferrets (Biggins et al. 2006d) as well as the effects of enzootic plague that may compromise habitat quality without being readily apparent (Biggins et al. 2010, Matchett et al. 2010).

Since few reintroduction sites have been able to meet the minimum 30 breeding adult criterion due to inherent biological capability and/or sylvatic plague epizootics, most active reintroduction sites have been maintained by frequent releases of captive-born animals (Table 5). Each year approximately 80-100 select kits are retained in the captive population to maintain a stable breeding age structure, and to minimize the loss of genetic diversity; any excess non-essential kits are allocated to reintroduction sites or used for research purposes (USFWS 2017). The allocation of excess kits is essential to starting new reintroduction sites, and allocations to existing reintroduction sites have utility in that they can 1) serve as a means of demographic rescue if the site is in imminent danger of extirpation and 2) ameliorate genetic drift-induced losses of genetic diversity in the short term at sites that are otherwise self-sustaining (Wisely 2006, Wisely et al. 2008). However, frequent augmentation to reintroduction sites is counterproductive to the ultimate goal of establishing self-sustaining, genetically diverse reintroduced populations that can acquire the ability to adapt to local environmental conditions and contribute to overall redundancy (Traill et al. 2010, IUCN/SSC 2013, Rosenfeld 2014). A more sustainable strategy may be to periodically augment self-sustaining reintroduced populations through translocation of other wild-born (or in some instances, captive-born) individuals (Wisely 2006, Wisely et al. 2008). Such a strategy would help foster the cultural transmission of important behaviors in reintroduced populations (Biggins 2000), as well as prevent phenotypic changes that may arise due to declines in genetic diversity (Wisely et al. 2008).

Table 5. Captive-born black-footed ferret kits allocated to active reintroduction sites for population augmentation purposes, 2009-2018 (not including initial releases during the first 3 years of site establishment).

Site	Year Established	Years Augmented	Total kits (males.females)
Shirley Basin, WY	1991	2012, 2017, 2018	26.25
UL Bend NWR, MT	1994	2009, 2013	17.9
Aubrey Valley/Double O Ranch, AZ	1996	2011, 2012, 2013, 2017, 2018	74.42
Coyote Basin, CO/UT	1999	2009, 2011, 2012, 2013, 2018	73.48
Lower Brule Reservation, SD	2006	2011, 2012, 2017, 2018	48.30
Butte Creek Ranches, KS	2007	2010, 2012, 2014, 2016, 2017	64.47
Wind Cave NP, SD	2007	2010, 2013, 2016	16.11
City of Fort Collins, CO	2014	2017, 2018	11.10
Crow Reservation, MT	2015	2018	6.4
TOTAL			**335.226**

Reintroduction sites vary in their ability to support black-footed ferret populations, primarily due to site size, level of conservation efforts (primarily sylvatic plague mitigation efforts), prairie dog density, drought and other abiotic factors, and the occurrence of sylvatic plague epizootics. Notably, large reintroduction sites located in white-tailed prairie dog habitat such as Shirley Basin, Wyoming, are typically not surveyed in their entirety, and actual population levels may be higher than reported (Grenier et al. 2007, Grenier et al. 2008). Sites such as Shirley Basin may be able to achieve resilience with fewer management inputs such as plague mitigation and population augmentation as a result of their large size and lower sylvatic plague transmission rates, possibly due to the low densities and loose colonial structure of white-tailed prairie dogs (Cully 1989, Cully and Williams 2001, Gasper and Watson 2001). Nonetheless, large white-tailed prairie dog reintroduction sites do experience sylvatic plague epizootics (Menkens and Anderson 1991, Anderson and Williams 1997, Seglund 2010), which can have population-level impacts on black-footed ferrets (Forrest et al. 1988, Wisely et al. 2008, Seglund 2010). Further investigations need to be conducted to assess plague dynamics, black-footed ferret persistence, and the efficacy of plague management efforts in these habitats (Biggins et al. 2010, Russell et al. 2019) to determine their resilience. Tools such as occupancy modeling (MacKenzie et al. 2003) may be more appropriate to assess black-footed ferret population levels in these habitats. See Table 3 for more detailed characteristics of each reintroduction site and its current and past performance.

3.4.3 Stressors Considered for Inclusion in Current Condition Analysis

The current condition of stressors affecting the black-footed ferret are provided in **Section 3.2 Factors Influencing Black-footed Ferret Condition**, which discussed disease, genetic fitness, drought, agricultural land conversion, recreational shooting of prairie dogs, poisoning of prairie dogs, range management, urbanization, and energy development. We did not carry forward all of these stressors into the current condition analysis. A stressor was considered in the current condition analysis if 1) the magnitude of the stressor across the potential range of the black-footed ferret was generally known, 2) a negative effect of the stressor has been quantified, and 3) the stressor was known to affect black-footed ferrets and/or their prairie dog prey at the species level, or if the stressor was known to have synergistic effects with other stressors (Table 6). These stressors are the main factors driving the current condition of the species. In some instances, stressors were combined due to their similarity of effects on black-footed ferret populations, such as prairie dog poisoning and recreational shooting of prairie dogs, as well as their similar roles as additive factors with respect to other stressors (e.g., sylvatic plague; Biggins and Eads 2019). In other cases, identified stressors were a subset of a broader category, such as sylvatic plague.

For a stressor to have a quantifiable negative effect on black-footed ferrets and/or their prairie dog prey, both exposure and response must occur. In some cases, such as energy development and urbanization, measures of exposure were available, but evidence suggests that black-footed ferrets and/or their prairie dog prey are relatively resilient to the stressor and do not exhibit a measurable negative response. A challenge unique to the black-footed ferret is a lack of data showing a link between population performance and stressor exposure, due primarily to the lack of adequate sample size needed to quantify such relationships; black-footed ferrets have been reintroduced at only 29 discrete locations, limiting the level of inference that can be achieved.

We acknowledge that some stressors likely have localized effects within some black-footed ferret reintroduction sites, but this SSA report seeks to quantify the black-footed ferret's viability at the species level. Disease (narrowly defined as sylvatic plague), genetic fitness, drought, and lethal control (a combined category of recreational shooting of prairie dogs and prairie dog poisoning) were carried forward in the current condition analysis because the magnitudes of these stressors within the potential range of the black-footed ferret are known, negative responses have been quantified, and the stressors have species-level effects, either singularly or in combination with other stressors (Figure 15). Effects from the stressors not carried forward in the current condition analysis (agricultural land conversion, range management, and urbanization) were not expected to have a measurable effect at the species level.

Table 6. Consideration of stressors for inclusion in the current condition analysis for the black-footed ferret. To be carried forward in the analysis, the magnitude of the stressor needs to be known, a negative response must be quantified, and the negative response must occur at the species level, either singularly or in combination with another stressor.

Stressor	**Magnitude Known?**	**Negative Response Quantified?**	**Species-level Response?**	**Carried Forward in Analysis?**
Plague (subset of Disease)	Yes	Yes	Yes	Yes
Genetic Fitness	Yes	Yes	Yes	Yes
Drought	Yes	Yes	Yes	Yes
Agricultural Land Conversion	Yes	Yes	No	No
Lethal Control of Prairie Dogs (combined category; see above)	Yes	Yes	Yes	Yes
Range Management	No	Yes	No	No
Urbanization	Yes	No	No	No
Energy Development	Yes	No	No	No

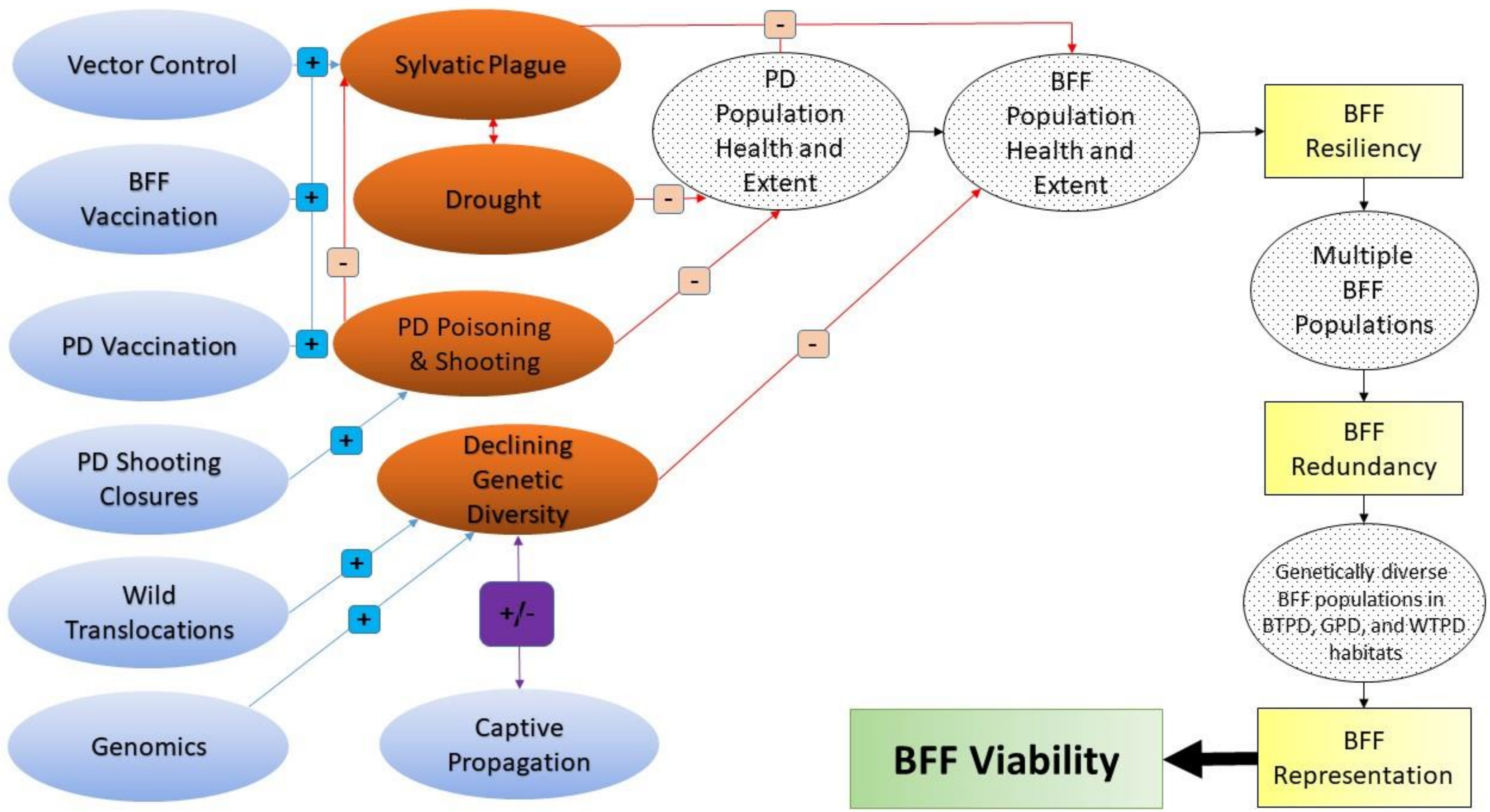

Figure 15. A detailed influence diagram modeling how key stressors and conservation efforts can affect the resilience of black-footed ferret populations. Stressors (orange polygons) decrease the health and extent of prairie dog populations and black-footed ferret populations. Conservation efforts (blue polygons) increase both prairie dog and black-footed ferret population health, and increase black-footed ferret population resiliency. The presence of multiple resilient black-footed ferret populations that are genetically diverse and located in diverse habitat types increases redundancy and representation, and overall black-footed ferret viability.

3.4.4 Analysis of Current Condition

To assist with the analysis of current condition for the black-footed ferret, we utilized an expert panel comprised of conservation professionals familiar with the conservation biology of the black-footed ferret to develop matrices describing the current resiliency of captive and reintroduced black-footed ferret populations. The matrices were developed by combining the stressors identified in **Section 3.4.3** with abundance and trend data (see **Sections 3.4.1 and 3.4.2**, above) and current and suggested conservation measures. The analysis units used in the matrices were locations of black-footed ferret captive breeding facilities (Table 2) and black-footed ferret reintroduction sites (Table 3). The categories used for the matrices are described below.

3.4.4.1 Current Resiliency of the Captive Black-footed Ferret Population

The classes used to evaluate the current resiliency of the captive black-footed ferret population are % whelping success (Figure 9), the mean number of kits born per litter (Figure 10), and the percentage of total kits weaned (Figure 12). These classes capture the level of breeding success, animal condition, and husbandry effectiveness for the six facilities housing the captive population, and were developed with the assistance of members of the Black-footed Ferret SSP®. While not stated explicitly, these classes are also an indirect measure of declining genetic diversity. Scores were assigned using the criteria shown in Table 7.

Table 7. Current resilience classes and scores used in the evaluation of the captive black-footed ferret population.

Parameter of Interest	Values for Score of 3 (high)	Values for Score of 2 (moderate)	Values for Score of 1 (low)
% Whelping success	>60%	40-59%	<40%
Mean # of kits/litter	>4	3-4	<3
% Kits weaned	>90%	80-89%	<80%

These classes were evaluated for each facility housing the captive population for the period 2009 to 2013 (Table 8) and 2014 to 2018 (Table 9). Scores were summed across categories to derive total resiliency class scores, which were classified as >7=high, 5-7=moderate, and <5=low. Scores generally declined in most classes for each facility between the two time periods evaluated.

Table 8. Current resiliency table for facilities housing the black-footed ferret SSP® population, 2009-2013. Numbers denote resiliency class scores (1=low, 2=moderate, and 3=high).

Facility	**% Whelping success**	**Mean # kits/litter**	**% Kits weaned**	**TOTAL SCORE**
National Black-footed Ferret Conservation Center	2	3	2	**7**
Smithsonian Conservation Biology Institute	3	3	3	**9**
Louisville Zoological Garden	3	3	3	**9**
Cheyenne Mountain Zoo	2	2	1	**5**
Phoenix Zoo	1	2	1	**4**
Toronto Zoo	2	3	2	**7**

Table 9. Current resiliency table for facilities housing the black-footed ferret SSP® population, 2014-2018. Numbers denote resiliency class scores (1=low, 2=moderate, and 3=high).

Facility	**% Whelping success**	**Mean # kits/litter**	**% Kits weaned**	**TOTAL SCORE**
National Black-footed Ferret Conservation Center	1	3	2	**6**
Smithsonian Conservation Biology Institute	3	3	2	**8**
Louisville Zoological Garden	2	2	1	**5**
Cheyenne Mountain Zoo	1	3	1	**5**
Phoenix Zoo	1	2	1	**4**
Toronto Zoo	1	2	2	**5**

3.4.4.2 Current Resiliency of the Reintroduced Black-footed Ferret Population

The classes used to evaluate the current resiliency of the reintroduced black-footed ferret population are the five-year mean number of breeding adult ferrets, the five-year mean ferret family rating (a biomass-based index of black-footed ferret habitat suitability incorporating prairie dog colony area and prairie dog density; see Biggins et al. 1993 and Biggins et al. 2006d for details), annual plague management level, annual black-footed ferret vaccination level, black-footed ferret population persistence, and level of prairie dog population protection. High, moderate, and low scores for each class are 3, 2, and 1, respectively; some classes included a value of zero if ferrets were not present at a reintroduction site, and others were weighted. An occupancy multiplier (1 for occupied, 0 for unoccupied) was used to prevent inflation of scores for unoccupied sites. Descriptions of the classes and scoring methodology used are found in Table 10.

Resiliency classes were evaluated for 29 discrete black-footed ferret reintroduction sites for the period 2014-2018. The 5-year mean number of breeding adults and ferret population persistence classes provide a measure of demographic performance, and potentially address the stressor of declining genetic diversity. The 5-year mean ferret family rating class provides a measure of habitat suitability, and how it is influenced by the stressors of drought, sylvatic plague, and prairie dog poisoning and shooting. The annual plague management level and annual ferret vaccination level classes directly address the stressor of sylvatic plague, and the level of prairie dog protection class addresses the combined stressor of prairie dog poisoning and shooting. Due to their importance to black-footed ferret population resilience, the 5-year number of breeding adults class was weighted by a factor of 10, and the 5-year mean ferret family rating and annual plague management level classes were weighted by a factor of 5. Adjusted current resiliency class scores were classified as 0 = Inactive, ≤ 33 = Low, > 33 and ≤ 50 = Moderate, > 50 = High (Table 11).

Table 10. Descriptions of resiliency class scores used in the evaluation of the reintroduced black-footed ferret population.

Class	Description and Scoring Methodology	Stressors Addressed
5-year Mean Number of Breeding Adults (from Fall surveys)	>30=high, 10-30=moderate, <10=low, 0=inactive/no value; **raw score weighted by a factor of 10**	Drought, sylvatic plague, declining genetic diversity
5-year Mean Ferret Family Rating	>100=high, 30-100-moderate, <30=low; **raw score weighted by a factor of 5**	Drought, sylvatic plague, prairie dog poisoning and shooting
Annual Plague Management Level	>50% of available acreage treated=high, ≤50% of available acreage treated or plague epizootic not documented at site=moderate, minimal or no plague management undertaken annually=low; **raw score weighted by a factor of 5**	Sylvatic plague
Annual Ferret Vaccination Level	>50% of population vaccinated each year=high, ≤50% of population vaccinated each year=moderate, minimal or no vaccination effort=low	Sylvatic plague
Ferret Population Persistence	self-sustaining=high, ≤1 population augmentation in 5 years=moderate, >1 population augmentation in 5 years=low, no ferrets present at site for the past 5 years=no value	Drought, sylvatic plague, declining genetic diversity
Level of Prairie Dog Protection	No lethal control permitted=high, lethal control regulated=moderate, lethal control unregulated=low	Prairie dog poisoning and shooting

Table 11. Current resiliency table for 29 black-footed ferret reintroduction sites, 2014-2018. Numbers denote resiliency class scores (0=inactive, 1=low, 2=moderate, and 3=high). Adjusted current resiliency is a weighted value that is the result of multiplying the 5-year mean # of breeding adults class by 10 and the 5-year mean ferret family rating and annual plague management level classes by 5, and adding these values to the remaining classes. Adjusted current resiliency rankings are as follows: 0 = Inactive, ≤ 33 = Low, > 33 and ≤ 50 = Moderate, > 50 = High

Site and Location	Prairie Dog Species	5-year mean # of breeding adults (10X)	5-year mean ferret family rating (5X)	Annual Plague Management Level (5X)	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD protection	Occupancy Multiplier (1 or 0)	Adjusted Current Resiliency
Conata Basin, SD	BTPD	3	3	3	3	3	3	1	69
UL Bend NWR, MT	BTPD	1	1	2	3	2	3	1	33
Ft. Belknap, MT	BTPD	1	1	2	3	1	2	1	31
Cheyenne River, SD	BTPD	1	2	1	1	1	1	0	0
BLM 40 Complex, MT	BTPD	0	1	1	1	0	1	0	0
Janos, MX	BTPD	0	2	1	1	0	1	0	0
Rosebud, SD	BTPD	1	2	1	1	1	1	0	0
Lower Brule, SD	BTPD	1	1	2	3	1	2	1	31
Wind Cave NP, SD	BTPD	1	2	2	3	1	3	1	37
Butte Creek Ranches, KS	BTPD	1	2	2	3	1	3	1	37
Northern Cheyenne, MT	BTPD	0	1	1	1	0	1	0	0
Vermejo BTPD, NM	BTPD	1	2	1	1	1	3	0	0
Grasslands NP, SK	BTPD	0	1	1	1	0	3	0	0
Walker Ranch, CO	BTPD	0	1	3	1	0	3	0	0
City of Fort Collins, CO	BTPD	1	1	3	3	1	3	1	37
North Holly, CO	BTPD	1	1	3	1	1	3	0	0
Liberty, CO	BTPD	1	1	3	1	1	3	0	0
Rocky Mountain Arsenal NWR, CO	BTPD	2	2	3	3	3	3	1	54

Site and Location	Prairie Dog Species	5-year mean # of breeding adults (10X)	5-year mean ferret family rating (5X)	Annual Plague Management Level (5X)	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD protection	Occupancy Multiplier (1 or 0)	Adjusted Current Resiliency
Bad River Ranch, SD	BTPD	1	1	2	1	1	3	0	0
Crow Reservation, MT	BTPD	1	1	2	2	1	2	1	30
South Holly, CO	BTPD	1	1	3	1	1	3	0	0
Moore Ranch, NM	BTPD	1	1	3	1	1	3	1	35
Aubrey Valley, AZ	GPD	2	3	2	2	1	2	1	50
Espee Ranch, AZ	GPD	1	2	2	1	1	2	0	0
Vermejo GPD, NM	GPD	1	1	1	1	1	3	0	0
Shirley Basin, WY	WTPD	2	3	1	2	2	2	1	46
Coyote Basin, CO-UT	WTPD	1	3	2	1	1	2	1	39
Wolf Creek, CO	WTPD	0	1	1	1	0	2	0	0
Meeteetse, WY	WTPD	1	2	3	3	1	2	0	41

3.5 Summary of Historical and Current Condition in terms of the 3Rs

According to our analysis of relevant data and through the development of condition classes to make these data comparable between analysis units, one of the six captive breeding facilities within the black-footed ferret captive population is in high condition, four are in moderate condition, and one is in low condition with respect to resiliency. Data from previous years (Table 8) suggest that the condition class values for most facilities have declined over time, and the long-term trend of declining whelping rates (Figure 9) may be the result of this phenomenon. While the overall condition of the black-footed ferret captive population can be considered resilient in that stable age structure and sex ratios have been maintained while maximizing the conservation of remaining genetic diversity (Wisely et al. 2003), recent trends may reflect a decline in the population's overall resiliency. The redundancy of the captive population (consisting of six captive breeding facilities) has remained unchanged for over 10 years. The captive population cannot increase its limited genetic representation due to its static number of founders, unless technologies such as iSCNT can be utilized to arrest the erosion of genetic diversity (Wisely et al. 2015).

Results for the reintroduced population indicate that two reintroduction sites are in high condition, eight are in moderate condition, four are in low condition with respect to resiliency, and 15 are inactive. Population trends are negative (Figure 11), and population levels have not kept pace with the rate at which new reintroduction sites have been added (Figure 12). Overall resiliency for this population is low, given the need to augment existing reintroduction sites regularly with excess animals from the captive population, and most importantly the need for continuous management inputs such as plague management and black-footed ferret vaccination to keep individual sites from succumbing to sylvatic plague epizootics. The redundancy of this population has been compromised in recent years, with only 14 of 29 reintroduction sites being classified as active. While this population does occur within the ranges of all three species of prairie dogs as it did historically, only one active population exists within Gunnison's prairie dog habitat, reducing overall population redundancy and ecological representation. Genetic representation is also limited, as ferrets that occupy most reintroduction sites are still closely related to ferrets from the captive population, primarily due to frequent population augmentations.

It is important for us to acknowledge that the black-footed ferret is a conservation-reliant species (Scott et al. 2010, Rohlf et al. 2014), and as such considerable management inputs are required to maintain both the captive and reintroduced populations of the species. These inputs include management and oversight of a captive breeding program, veterinary care and animal husbandry (USFWS 2017), maintenance of a preconditioning program (Biggins et al. 1998, USFWS 2017), and plague management and ferret vaccination programs at individual reintroduction sites. This past and ongoing management has been crucial to maintaining the current levels of resiliency, redundancy, and representation of the black-footed ferret.

Chapter 4. Future Condition

In this chapter, we project the future condition of the six captive breeding facilities within the black-footed ferret SSP® population, and the 29 reintroduction sites comprising the reintroduced black-footed ferret population. This analysis includes five potential scenarios of changes in stressors (due in part to climate change) and conservation efforts. The scenarios are evaluated over two timeframes (10 years and 20 years) in an effort to predict how viability of the black-footed ferret may change in the future. These timeframes were chosen due to the short generation time of the black-footed ferret (3-4 years), the high level of variation experienced by populations in response to drought, sylvatic plague, and other factors, and the small numbers of individuals at several reintroduction sites. Many reintroduction sites have a high likelihood of experiencing local extirpations (see Figure 13) due to their small local population sizes, and as a result are often re-initiated through the release of captive-reared animals on a relatively frequent (3 to 7 years) basis. In addition, the known annual loss of genetic diversity (currently estimated to be 0.17 percent per year; see Graves et al. 2018) makes it incumbent on managers to identify potential conservation practices as quickly as possible. This high level of variability complicated analyses using longer timeframes, so we attempted to address known stressors and their effects on black-footed ferret populations using these shorter timeframes.

4.1 Climate Change

Greenhouse gas (GHG) emissions increased at an unprecedented rate during the 20th century, resulting in global climate change characterized by warming atmospheric and ocean temperatures, diminishing coverage of snow and ice, and rising sea levels (Intergovernmental Panel on Climate Change (IPCC) 2014). Scientists use a variety of climate models, which include consideration of natural processes and variability as well as various scenarios of potential levels and timing of GHG emissions, to evaluate the causes of changes already observed and to project future changes in temperature and other climate conditions (Meehl et al. 2007, Ganguly et al. 2009, Prinn et al. 2011). Combinations of models and emission scenarios yield very similar projections of increases in the most common measure of climate change, average global surface temperature, until approximately 2030. Although projections of the magnitude and rate of warming differ after 2030, the overall trajectory of all of the projections is one of increased surface temperature through the end of this century, even for projections based on scenarios that assume GHG emissions will stabilize or decline. Regardless of the projections in question, there is strong evidence that average surface temperatures will continue to increase through the 21st century, and the magnitude and rate of this change will be substantially influenced by the extent of GHG emissions (Meehl et al. 2007, Ganguly et al. 2009, Prinn et al. 2011, IPCC 2014).

It is important for us to include the potential effects of climate change in our analysis of the future condition of the black-footed ferret, primarily due to its effects on two primary stressors affecting black-footed ferret populations, drought and sylvatic plague (Facka et al. 2010, Eads et al. 2016). To do this, we used climate change data obtained from the USGS National Climate Change Viewer (NCCV; Alder and Hostetler 2013). The NCCV averages the results of 33 global climate change (GCM) models and provides predictions for two GHG emissions scenarios called Representative Concentration Pathways (RCP). The two scenarios (RCP4.5 and RCP8.5) are projected through three future time periods (2025 to 2049, 2050 to 2074, and 2075 to 2099), which in turn are compared against a reference period from 1981 to 2005 (Alder and Hostetler 2013). The two GHG emissions scenarios used in the NCCV come from the latest IPCC report (IPCC 2014). The RCP4.5 scenario is an intermediate emissions scenario where atmospheric CO_2 concentrations are expected to equal approximately 650 ppm by the year 2099. The RCP8.5 scenario is more aggressive, with atmospheric CO_2 concentrations rising to approximately 1370 ppm by 2099. For comparison, current atmospheric CO_2 concentrations are approximately 400 ppm (Alder and Hostetler 2013).

To evaluate climate predictions throughout the potential range of the black-footed ferret, we developed NCCV model predictions at the scale of individual counties, and selected counties where reintroduction sites for black-footed ferrets have occurred (28 counties in 8 states). For reintroduction sites in Canada and Mexico, which are close to the U.S. border, we selected the U.S. counties located closest to the reintroduction sites (2 counties in 2 states). Although this frame of analysis is somewhat restrictive, the distribution of black-footed ferret reintroduction sites covers most of its potential range (Figure 2), with the exception of the eastern portion. To address this shortcoming, we selected eight additional counties in the states of Kansas, Nebraska, North Dakota, Oklahoma, and Texas where potential reintroduction sites have been identified (Luce 2006), to enhance the geographic coverage of our analysis. A total of 38 counties located in 12 states were used to develop NCCV model predictions (Table 12). Since the end points of the two time periods of interest we identified for this report (2029 and 2039) both fall within the NCCV 2025-2049 climatology period, we differentiated between the two points by using the time series function in the NCCV. We used the time series function to identify discrete values of parameters of interest by year in the model, which allowed us to differentiate between the two points quantitatively through trend analysis. We used different emission scenarios (RCPs) depending on the parameters set forth in each of our future scenarios (see **Section 4.2.2 Descriptions of Future Scenarios**).

Table 12. United States counties used to develop National Climate Change Viewer projections of climate change within the potential range of the black-footed ferret.

State	Counties of Interest
Arizona	Coconino, Mojave
Colorado	Adams, Baca, Larimer, Moffat, Prowers, Pueblo, Weld
Kansas	Barber, Logan
Montana	Big Horn, Blaine, Phillips, Powder River, Yellowstone
Nebraska	Garden
New Mexico	Colfax, Hidalgo, Mora
North Dakota	McKenzie, Sioux
Oklahoma	Beaver
South Dakota	Custer, Dewey, Lyman, Pennington, Stanley, Todd, Ziebach
Texas	Brewster, Lipscomb, Sherman
Utah	Uintah
Wyoming	Albany, Carbon, Natrona, Park

Across both of our future climate scenarios, mean annual maximum temperature is expected to increase over time within the potential range of the black-footed ferret, with the magnitude of the increase amplified under the RCP8.5 emissions scenario. While most of the counties of interest followed the general pattern of increasing spring precipitation and decreasing summer precipitation, some counties in the southern portion of the range may experience reduced spring precipitation as well, with little to no change in summer precipitation. Across the potential range, soil water storage is expected to decrease, and evaporative deficit is expected to increase. Evaporative deficit is the difference between water availability in the soil and water lost to evapotranspiration. As evaporative deficit increases, the landscape becomes drier and drought conditions increase in severity and duration.

Because drought and plague are significant stressors in terms of their effects on black-footed ferret habitat quality, we focused on evaporative deficit instead of annual maximum temperature or precipitation levels as a measure of climate change that may have the greatest effect on the viability of the species. Plague dynamics are thought to be influenced by drought, although the mechanisms are not well understood and results are sometimes conflicting (Snall et al. 2009, Eads et al. 2016, Eads and Biggins 2017). The effects of more commonly used measures such as increased temperature and precipitation on plague can confound each other, and the effects of increased temperature override increased precipitation in some models (Stewart et al. 2004). This phenomenon explains the expected decrease in soil moisture and increase in evaporative deficit within the potential range of the black-footed ferret in the future. These effects suggest that at the potential range scale, black-footed ferret habitat may become drier in the future as a result of climate change (Stewart et al. 2004, Dai 2011). This effect is likely amplified under increasing levels of GHG emissions (Alder and Hostetler 2013). For these reasons, we utilized measures of evaporative deficit for our predictions of drought conditions that may affect the viability of the black-footed ferret in the future.

4.2 Analysis of Future Condition

4.2.1 Acknowledgment of Uncertainty

Climate models are useful in that they allow us to make predictions of how climate may change in the future, but their results should be interpreted carefully. Models are mathematical representations of what can happen, but they do not always accurately predict future events. The accuracy of climate models has improved in recent years, but projections for precipitation remain less reliable than those for surface temperature (O'Gorman and Schneider 2009, Trenberth 2011, IPCC 2014). For our analysis of the black-footed ferret's future condition, we acknowledge the inherent uncertainty associated with climate modeling, particularly with respect to the frequency and severity of drought, one of the primary stressors with respect to black-footed ferret habitat quality. We also recognize that these models represent some of the best available scientific data that we can utilize for projecting the species' future condition.

Several studies have predicted an increase in precipitation variability in the future due to the effects of climate change, primarily in the form of more frequent extreme precipitation events (O'Gorman and Schneider 2009, Trenberth 2011, IPCC 2014). An increase in extreme precipitation events does not necessarily equate to a wetter environment, as this escalation is offset by increasing temperatures and rates of evapotranspiration (Trenberth 2011). Rather, this represents a redistribution of annual precipitation that leads to a drier landscape overall (Trenberth 2011). While there is good evidence for increased precipitation variability in the future, unfortunately there is not a metric available to measure this increase. This is important in the context of future condition analyses involving plague, as epizootics may follow short-term periods of dramatic variation in timing and amount of precipitation (Eads et al. 2016, Eads and Biggins 2017). Due to this limitation, we used conservative judgment and assumed that increased precipitation variability only served to increase the frequency of plague epizootics under future condition scenarios using the RCP8.5 climate change scenario.

Uncertainties also exist with respect to the efficacy of conservation efforts in the future. Due to the considerable management inputs required to maintain both the captive and reintroduced black-footed ferret populations and the species' high susceptibility to plague, we assume that some form of plague management (a combination of vector control, oral vaccine baits, and individual ferret vaccination) is required to prevent the extirpation of the reintroduced population. As noted above (see **Section 3.4.2.2 Reintroduced Black-footed Ferret Population**), larger black-footed ferret reintroduction sites in white-tailed prairie dog habitat may exhibit greater resiliency with respect to susceptibility to sylvatic plague, so these sites may not require the level of plague management that sites located in other habitats require. At present limited resources prevent the implementation of plague management at every reintroduction site, and we cannot predict the availability of plague management resources in the future. The plague management data presented in Table 1 is considered a baseline level of plague management, with approximately 20% of the habitat currently occupied by the reintroduced black-footed ferret receiving some form of plague management. Additionally, it is likely that the efficacy of various plague management techniques are not equal, and additional research on formulation, timing of application, and synergistic effects is needed (Tripp et al. 2014, Tripp et al. 2017).

4.2.2 Description of Future Condition Scenarios

We used the condition classes developed for the captive and reintroduced black-footed ferret populations (Tables 7 and 10, respectively) to frame our future condition analysis for both populations. These condition classes were informed by abundance and trend data for both populations (**Section 3.4.2**) and identified stressors (**Section 3.4.3**). For our future condition analysis, we constructed five scenarios focused on changes in climate, levels of conservation efforts, reintroduction site habitat quality and quantity (reintroduced population only), and production levels of black-footed ferret kits from both the captive and reintroduced populations. These scenarios are meant to represent the wide range of future conditions that could occur in the black-footed ferret's potential range. We projected each scenario to two time periods in our analysis of future condition, 10 and 20 years from the present. Depending on the scenario, the RCP4.5 or RCP8.5 emission scenarios were used for the climatology period of 2025-2049.

Continuation Scenario

This scenario is a continuation of current conditions, with management of existing reintroduction sites and captive breeding facilities continuing at the same scale and intensity. New reintroduction sites are added at the same rate as observed during the past five years (approximately two per year), and new sites are the mean size of sites added during the past five years (975 ha). The current baseline of approximately 20% of all active habitat receives plague management each year, and plague epizootics occur at their current magnitude and frequency. Ferret vaccination efforts at reintroduction sites continue at their current level, and prairie dog protection levels are unchanged. Limited incentive programs are available to encourage non-federal landowners to participate in black-footed ferret recovery. Captive population reproduction metrics (whelping success, mean number of kits born per litter, and weaning %) continue to follow current trends, and 15 wild-born kits are available each year for translocation from existing to new reintroduction sites. Greenhouse gas emissions follow the RCP4.5 scenario.

Pessimistic Scenario

Under this scenario, 10% of active habitat receives plague management each year, and plague epizootics increase in magnitude and frequency. Ferret vaccination rates do not exceed 50% for any reintroduction site, and no new reintroduction sites are developed. Prairie dog protection levels are unchanged. Incentive programs are not available for non-federal landowners. Captive population reproduction metrics decline by 10% relative to 5-year mean values, and no wild-born kits are available for translocation. Greenhouse gas emissions follow the RCP8.5 scenario.

Disastrous Scenario

This scenario represents a significant loss in management intervention capability, with only 5% of active habitat receiving plague management each year. Plague epizootics increase in magnitude and frequency. Ferret vaccination rates do not exceed 25% for any reintroduction site, and no new reintroduction sites are developed. Prairie dog protection levels decrease, with no reintroduction sites except for those associated with National Parks and National Wildlife Refuges having complete prohibitions on lethal control. Incentive programs are not available for non-federal landowners. Captive population reproduction metrics decline by 50% relative to 5-year mean values, and no wild-born kits are available for translocation. Greenhouse gas emissions follow the RCP8.5 scenario.

Optimistic Scenario

This scenario represents an increase in management intervention capability, with ≥50% of active habitat receiving plague management each year. Five new reintroduction sites capable of supporting ≥30 breeding adults each are added to the reintroduced population by the year 2029. Prairie dog protection levels are unchanged, and >50% of new reintroduction sites added have complete prohibitions on lethal control of prairie dogs. Incentive programs for non-federal landowners are available throughout the potential range. Captive population reproduction metrics increase by 20% relative to 5-year mean values, and ≥30 wild-born kits are available for translocation each year. Greenhouse gas emissions follow the RCP4.5 scenario.

Transformation Scenario

This scenario includes technological breakthroughs and increased resource availability for management intervention. Plague management is implemented annually on ≥75% of active habitat due to the development of additional cost-effective management tools, and five new reintroduction sites capable of supporting ≥100 breeding adults each are added to the reintroduced population by the year 2029. Prairie dog protection levels are unchanged, and >75% of new reintroduction sites added have complete prohibitions on lethal control of prairie dogs. Incentive programs for both non-federal landowners as well as lessees of federal lands are available. Captive production metrics increase by 30% relative to 5-year mean values, and captive-reared animals exhibit some resistance to plague through the use of genomic technologies. At least 50 wild-born kits are available for translocation each year. Greenhouse gas emissions follow the RCP4.5 scenario.

4.2.3 Predicting Future Condition

We predicted the future conditions of each analysis unit (6 captive breeding facilities and 29 reintroduction sites) based on a combination of current population trends and variations of stressors and conservation efforts specified in our future scenarios. Specifically, we predicted how these factors influenced the three classes developed for our current resiliency analysis for the captive black-footed ferret population (Table 7), and the six classes developed for our current resiliency analysis for the reintroduced black-footed ferret population (Table 10). For the three classes associated with the captive population, we considered current population trends, conservation efforts, and the stressor of genetic fitness. For the six classes associated with the reintroduced population, we considered current population trends, conservation efforts, and the stressors of plague, genetic fitness, lethal control of prairie dogs, and drought.

Drought and its effects on black-footed ferret habitat quality and plague occurrence were assessed by looking at future projections of evaporative deficit in each of the scaled-down climate models described in **Section 4.1 Climate Change**. Although the scope of our analysis (conditions at 2029 and 2039) falls within the same NCCV climatology period (2025-2049), we discerned changes in evaporative deficit between the two points by using the time series function in the NCCV. Use of the time series function enabled us to identify discrete values of evaporative deficit by year in the model, which enabled us to differentiate between the two points quantitatively through trend analysis for each of our counties of interest. We also evaluated trend for evaporation deficit over the entire 2019-2039 interval, and noted instances where model results changed in significance between different climate scenarios (1981-2010, RCP4.5, and RCP8.5).

We scored each of the resiliency classes in our future condition analysis in the same manner as our current resiliency analyses for the both the captive and reintroduced black-footed ferret populations. For the reintroduced population, we weighted resiliency classes in the same manner as the current resiliency analysis (see **Section 3.4.4.2** and Tables 10 and 11). For future scenarios that included the addition of reintroduction sites, we did not add them as discrete analysis units to the 29 current units in our evaluation of resiliency; rather, we evaluated their contribution in a qualitative sense to overall species redundancy and representation.

4.2.4 Results of Future Condition Analysis

In this section, we present the results of our future condition analysis under five scenarios, 10 and 20 years into the future. These analyses follow the same scoring methodologies described in

Sections 3.4.4.1 and 3.4.4.2, and results are summarized in Tables 13 and 14 below. Full future condition tables with results for each condition class, under each scenario and at each time point, are included in the Appendix.

Table 13. Summary of future condition analysis results for the captive black-footed ferret population under five scenarios during two time periods. Numbers denote resiliency class scores (<5=low, 5-7=moderate, and >7=high).

Facility	Continuation Scenario		Pessimistic Scenario		Disastrous Scenario		Optimistic Scenario		Transformation Scenario	
	2029	2039	2029	2039	2029	2039	2029	2039	2029	2039
National Black-footed Ferret Conservation Center	6	6	4	4	3	3	8	9	9	9
Smithsonian Conservation Biology Institute	8	7	5	5	3	3	9	9	9	9
Louisville Zoological Garden	5	4	5	4	3	3	8	8	9	9
Cheyenne Mountain Zoo	5	5	4	4	3	3	8	8	9	9
Phoenix Zoo	3	3	3	3	3	3	5	6	9	9
Toronto Zoo	5	4	4	4	3	3	8	8	9	9

Table 14. Summary of future condition analysis for the reintroduced black-footed ferret population under five scenarios during two time periods. Numbers in each cell denote adjusted future resiliency class scores (0 = Inactive, ≤ 33 = Low, > 33 and ≤ 50 = Moderate, > 50 = High; see Table 11 for description of scoring methodology)

Site and Location	Prairie Dog Species	Continuation Scenario		Pessimistic Scenario		Disastrous Scenario		Optimistic Scenario		Transformation Scenario	
		2029	2039	2029	2039	2029	2039	2029	2039	2029	2039
Conata Basin, SD	BTPD	69	69	48	48	41	41	69	69	69	69
UL Bend NWR, MT	BTPD	33	33	0	0	0	0	53	53	54	54
Ft. Belknap, MT	BTPD	31	31	0	0	0	0	46	46	69	69
Cheyenne River, SD	BTPD	0	0	0	0	0	0	46	46	69	69
BLM 40 Complex, MT	BTPD	0	0	0	0	0	0	35	35	44	44
Janos, MX	BTPD	0	0	0	0	0	0	0	0	69	69
Rosebud, SD	BTPD	0	0	0	0	0	0	45	45	69	69
Lower Brule, SD	BTPD	31	31	30	30	0	0	37	37	52	52
Wind Cave NP, SD	BTPD	37	37	31	31	0	0	43	43	54	54
Butte Creek Ranches, KS	BTPD	37	37	31	31	0	0	53	53	63	63
Northern Cheyenne, MT	BTPD	0	0	0	0	0	0	28	28	46	46
Vermejo BTPD, NM	BTPD	0	0	0	0	0	0	45	30	69	69
Grasslands NP, SK	BTPD	0	0	0	0	0	0	36	36	43	43
Walker Ranch, CO	BTPD	0	0	0	0	0	0	35	35	53	53
City of Fort Collins, CO	BTPD	37	37	31	31	0	0	37	37	44	44
North Holly, CO	BTPD	0	0	0	0	0	0	0	0	43	43
Liberty, CO	BTPD	0	0	0	0	0	0	0	0	43	43
Rocky Mountain Arsenal NWR, CO	BTPD	54	54	47	47	41	41	54	54	64	64
Crow Reservation, MT	BTPD	30	0	0	0	0	0	30	30	46	46
South Holly, CO	BTPD	0	0	0	0	0	0	0	0	37	37
Bad River Ranch, SD	BTPD	0	0	0	0	0	0	30	30	54	54
Moore Ranch, NM	BTPD	0	0	0	0	0	0	0	0	37	37
Aubrey Valley, AZ	GPD	45	45	36	35	0	0	61	51	53	68
Espee Ranch, AZ	GPD	0	0	0	0	0	0	35	30	52	52
Vermejo GPD, NM	GPD	0	0	0	0	0	0	0	0	53	53
Shirley Basin, WY	WTPD	46	46	37	41	35	35	51	51	68	68
Coyote Basin, CO-UT	WTPD	39	33	29	24	0	0	51	46	53	68
Wolf Creek, CO	WTPD	0	0	0	0	0	0	34	34	52	57
Meeteetse, WY	WTPD	41	41	35	35	23	0	52	52	68	68

Results: Continuation Scenario

A continuation of current management practices but under increasing levels of GHG under the RCP4.5 scenario leads to continued declines in resiliency for the reintroduced black-footed ferret population, while declining genetic fitness contributes to lower levels of resiliency for the captive black-footed ferret population. By extrapolating current trends, in 10 years we project that the Phoenix Zoo will decline from moderate to low condition in mean number of kits born per litter, but overall resiliency condition class does not change. Over a 20-year timeframe, we project that the Toronto Zoo will move from moderate to low resiliency condition due to continued declines in mean number of kits born per litter, and the Smithsonian Conservation Biology Institute will move from high to moderate condition due to declining whelping success.

For the reintroduced black-footed ferret population, in 10 years we project that the effects of increased drought will cause one site (Aubrey Valley/Double O Ranch) to decline in 5-year mean family ferret rating, reducing its overall score but keeping it in the moderate resiliency class. Increased drought will also hinder the recovery of extirpated sites in the southern portion of the potential range (Vermejo Ranch BTPD, Walker Ranch, North Holly, South Holly, and Liberty), preventing their reestablishment using captive-born or wild translocated animals. Due to drought and its vulnerability to demographic stochasticity because of its small size, we project that the Moore Ranch site will become inactive. In 20 years, we predict that increasing drought effects will reduce ferret family rating values at the Coyote Basin reintroduction site, reducing its overall score but keeping it in the moderate resiliency class. During this time period, we also predict that the Crow Reservation site becomes inactive, due a lack of availability of captive-born kits (see discussion below) for population augmentation, and erosion of ferret family rating due to increasing drought effects.

This scenario calls for the establishment of an average of two reintroduction sites per year averaging 975 ha. Given drought effects and declining availability of captive-born kits, this rate of reintroduction site recruitment is likely not sustainable even in a 10-year planning horizon, regardless of the availability of incentives for non-federal landowners. Moreover, sites of this size are unlikely to contribute appreciably to long-term redundancy and representation due to their demonstrably high extinction rates (see **Section 3.4.4.2**).

Synopsis: Continuation Scenario

In the Continuation Scenario, both the captive and reintroduced black-footed ferret populations will continue to persist during both timeframes, albeit with slightly reduced resiliency and redundancy. Current trends, coupled with predicted declines in genetic fitness, will cause a reduction the resiliency of the captive population, due primarily to declines in whelping success and mean number of kits per litter. For the reintroduced population, drought will erode ferret family rating values, but sites will maintain their current resiliency levels for the most part. Smaller, less resilient sites may become extinct due to demographic stochasticity and a lack of availability of captive-born kits for augmentation purposes, but wild-born kits from sites such as Rocky Mountain Arsenal NWR may be able to partially meet reintroduction site augmentation needs. Overall, both the captive and reintroduced black-footed populations retain some degree of resiliency, with some loss of redundancy in the reintroduced population due to site extinctions. Representation is largely unchanged, although the continued erosion of genetic diversity in the captive population reduces overall representation in a genetic context.

Results: Pessimistic Scenario
This scenario represents a general increase in the level of stressors, as well as a decrease in conservation efforts and captive population performance. Under the 10-year planning horizon, the resiliency scores for the captive black-footed ferret population are reduced markedly, with only two of the six facilities in moderate condition and the remaining four facilities in low condition. The captive population would not be able to provide any kits for release at reintroduction sites, and facilities would be challenged to maintain appropriate sex and age structure and mean kinship criteria under this scenario. At 20 years, the Louisville Zoological Garden moves from moderate to low condition, leaving the Smithsonian Conservation Biology Institute as the only facility in moderate condition with respect to resiliency.

For the reintroduced population, plague would greatly increase in magnitude as a stressor, given reduced resources to implement plague management, a lower ferret vaccination rate, and increased year-to-year variability in precipitation causing more frequent epizootics. For the 10-year planning horizon, no sites are in high resiliency condition, four sites are in moderate condition, six sites are in low condition, and 19 sites are inactive. Conditions worsen for the 20-year planning horizon as drought conditions, particularly in the southern and western portions of the potential range, continue to erode mean ferret family rating. With increasing precipitation variability, plague epizootics become more frequent. At 20 years, the numbers remain the same for all resiliency condition classes, but overall scores of individual sites continue to decline.

Synopsis: Pessimistic Scenario
In the Pessimistic Scenario, the captive black-footed ferret population experiences a significant decline in population performance, with no kits available for release at reintroduction sites and the beginnings of demographic breakdown due to a limited number of kits available for retention in the breeding population. For the reintroduced population, the effects of limited conservation efforts, declining habitat quality due to drought, and more frequent plague epizootics reduce the reintroduced population to only 10 active reintroduction sites, with most of these sites in the low resiliency condition category. While both populations retain a degree of resiliency, it is greatly reduced relative to the continuation scenario. Redundancy remains the same for the captive population, but declines for the reintroduced population due to site extinctions. As genetic diversity continues to decline in the captive population and few reintroduction sites remain in

Gunnison's and white-tailed prairie dog habitat, ecological and genetic representation likewise continue to decline.

Results: Disastrous Scenario

This scenario represents a virtual end to conservation efforts, and an inability to maintain viable populations in either captive or reintroduced settings. Under this scenario at both 10 and 20-year benchmarks, all of the facilities within the captive population are in low resiliency condition, and production levels are no longer sufficient to maintain a stable sex and age structure. No captive-born kits are available for release at reintroduction sites. For the reintroduced population, the combined effects of declining habitat quality due to drought and increased lethal control of prairie dogs, more frequent plague epizootics due to increased precipitation variability, and low ferret vaccination rates render this population functionally extinct, with only the Conata Basin-Badlands, Rocky Mountain Arsenal, Shirley Basin, and Meeteetse sites remaining active in 2029. Due to its smaller size, reduced ferret family rating, and more frequent epizootics of plague, we project that the Meeteetse site becomes inactive by 2039.

Synopsis: Disastrous Scenario

The Disastrous Scenario represents a significant challenge to black-footed ferret recovery efforts, with a severely compromised captive population that can no longer meet genetic diversity maintenance goals (Ballou and Oakleaf 1989). In this scenario, the reintroduced population in effect becomes the founder population, albeit with low genetic diversity and limited representation, as evidenced by occurrence in only black-tailed and white-tailed prairie dog habitat. For both populations, resiliency and redundancy are greatly reduced, as some of the captive facilities may not be able to breed ferrets successfully, and only three reintroduction sites remain active.

Results: Optimistic Scenario

This scenario represents a turnaround in population performance for the captive breeding population, with five facilities reaching high resiliency condition and one facility in moderate condition by 2029. This is the result of a 20% increase in whelping success, mean number of kits born per litter, and percentage of kits weaned. These improvements, due in part to revised husbandry and pairing methodologies and higher success of assisted reproductive technologies such as artificial insemination, continue through 2039, improving the overall resiliency scores for the National Black-footed Ferret Conservation Center and the Phoenix Zoo.

For the reintroduced population, targeted allocation of increased levels of plague management resources enable managers to reinitiate recovery efforts at 10 existing reintroduction sites, and increase the biological potential of existing active sites by 2029. Under this scenario, eight sites are in high resiliency condition, 12 are in moderate condition, and three sites are in low condition. Six sites remain inactive, due to allocation of resources to other sites having greater potential to meet the minimum recovery criterion of ≥30 breeding adults. The addition of five new reintroduction sites meeting this criterion increases the redundancy of the reintroduced population as well as its genetic and ecological representation, and is made possible by the availability of kits from both the captive population as well as translocations from existing reintroduction sites. The gains made in the overall condition of the reintroduced population are offset somewhat by increasing drought, particularly in the southern and western portions of the potential range. These effects become more evident by 2039, with the Espee Ranch and Vermejo BTPD reintroduction sites moving from moderate to low resiliency condition, and the Coyote Basin reintroduction site moving from high to moderate condition.

Synopsis: Optimistic Scenario

The Optimistic Scenario represents gains in resiliency and representation for the captive black-footed ferret population, and gains in resiliency, redundancy, and representation for the reintroduced population. These gains are realized through the availability of resources for conservation efforts, but are tempered somewhat by worsening drought conditions in portions of the potential range.

Results: Transformation Scenario

This scenario entails significant gains in population performance for both the captive and the reintroduced black-footed ferret populations, made possible by technological advances in captive breeding techniques and plague management. Gene pool enrichment, made possible through iSCNT, brings all captive breeding facilities into high overall resiliency condition by 2029, and these gains are maintained through 2039 due to evolving technologies.

For the reintroduced population, the greater availability of effective plague management tools enables managers of most reintroduction sites to implement plague management, and overall resiliency increases as a result. Larger sites capable of supporting ≥30 breeding adults are prioritized for plague management, and plague management is also implemented on smaller sites with research or cultural values. Widespread implementation of plague management, availability of incentive programs, and high levels of prairie dog population protection bring 20 reintroduction sites into high resiliency condition, with the remaining 9 sites in moderate condition. The addition of five new reintroduction sites capable of supporting ≥100 breeding adults increases redundancy and representation for the reintroduced population, and is made possible by the availability of kits from both the captive population as well as translocations from existing reintroduction sites. These gains in population viability are offset slightly by increasing drought, particularly in the southern and western portions of the potential range; by 2039 the Aubrey Valley, Espee Ranch, Vermejo BTPD, Vermejo GPD, Coyote Basin, and Wolf Creek reintroduction sites all decline in overall condition, but retain their overall condition classes.

Synopsis: Transformation Scenario
The Transformation Scenario represents a "best case" scenario in that technological advances greatly enhance the ability to manage both the captive and reintroduced populations, and sufficient resources are available to implement these advances. The resiliency of both populations is greatly enhanced, and redundancy in the reintroduced population is increased substantially. Representation is increased through the inclusion of new genetic material in the captive population, as well as through the addition of new reintroduction sites and the reinitiation of formerly inactive sites throughout the potential range of the species.

Chapter 5. Species Viability

This report describes what the black-footed ferret needs to achieve viability (Chapter 2), and evaluates the current condition of the species in relation to those needs (Chapter 3). This report also forecasts how the condition of the black-footed ferret may change in relation to those needs under five different scenarios (Chapter 4). In this chapter, we synthesize the results from our historical, current, and future analyses and discuss the potential future viability of the black-footed ferret. We assess the viability of the species by evaluating its ability persist into the future in the context of the 3Rs.

5.1 Resiliency

For a species that nearly became extinct (Lockhart et al. 2006), black-footed ferret populations have displayed remarkable resiliency in the face of numerous stressors. This resiliency has been achieved through considerable management inputs, including intensive and extensive captive breeding and reintroduction programs. The most significant challenges to black-footed ferret viability in the wild are sylvatic plague, and a lack of suitable habitat (CBSG 2004). Sylvatic plague is a non-native disease that is lethal to ferrets and their prairie dog prey, and requires management intervention in order to prevent the extirpation of the black-footed ferret reintroduced population. The current conditions of individual reintroduction sites, the analysis units we used for the reintroduced population, illustrate the challenges posed by plague. Since reintroduction efforts began in 1991, black-footed ferrets have been reintroduced at 29 discrete reintroduction sites. Of these 29 sites, two are currently in high resiliency condition, eight are in moderate condition, four are in low condition, and 15 are inactive. With the exception of the two sites in high condition and one site in moderate condition, periodic releases of animals from the captive population are needed to maintain active reintroduction sites. The inactive sites experienced plague epizootics, which eliminated habitat and resulted in direct black-footed ferret mortality. Black-footed ferret population resiliency, at least in the case of the reintroduced population, depends heavily on management interventions in the form of plague management and population augmentation using captive-born animals. Since most black-footed ferret reintroduction sites currently contain relatively small numbers of animals (range of 1 to 119; see

Table 3) and many are found in sub-optimal habitat, their ability to tolerate natural, annual variation in their environment in their current condition is limited.

Although it is buffered from external stressors such as plague and variable environmental conditions, the captive black-footed ferret population also exhibits limited resiliency due to its small (N=7) founder population and resultant low genetic diversity. The captive population, which numbers 301 animals, and is split between six captive breeding facilities (Table 2), currently has one facility in high resiliency condition, four in moderate condition, and one in low condition. Like the reintroduced population, the captive population requires significant management intervention for its maintenance.

Since the black-footed ferret is a conservation-reliant species, our analysis of future resiliency centered on the requirement for ongoing management of both the captive and reintroduced populations, and the degree to which management intervention might vary under differing circumstances. Resiliency for individual analysis units (reintroduction sites and captive breeding facilities) improved in the Optimistic and Transformation scenarios, while the Continuation, Pessimistic, and Disastrous scenarios resulted in losses of resiliency relative to current conditions. The only scenario in which management intervention is potentially reduced is the Transformation scenario, where advances in genomics may potentially offset the need for annual plague management activities.

5.2 Redundancy

As noted above, black-footed ferret populations were formerly widespread, occurring in conjunction with three species of prairie dogs in 12 present-day states. Although exact numbers of individual populations are not known, black-footed ferret specimens have been recorded from 128 of 513 counties within the historic range of the three species of prairie dogs (Anderson et al. 1986). While counties do not equate to populations, black-footed ferrets occurred in several discrete locations historically. At present, black-footed ferrets are found at six captive breeding facilities, and 14 reintroduction sites. The number of projected reintroduction sites in our analysis of future redundancy ranged from 10 (Disastrous Scenario, 20 year timeframe) to 34 (Transformation Scenario, 20-year timeframe) for the reintroduced population, and remained at six breeding facilities for the captive population in all scenarios. In the latter instance, some of the captive breeding facilities under the Disastrous Scenario may lose the ability to produce any black-footed ferrets in captivity, although the exact number is not known.

Climate effects and availability of conservation measures influenced the level of redundancy observed for the reintroduced black-footed ferret population, and genetic diversity influenced the level of redundancy for the captive population. Under all scenarios, at least some analysis units persisted, but their resiliency is questionable.

5.3 Representation

A species' representation is measured by evaluating its genetic, morphological, behavioral, and ecological diversity within and among populations across its range. Data generated from the study of the last wild black-footed ferret population near Meeteetse, Wyoming and analysis of museum specimens suggests that isolation of subpopulations likely occurred throughout the range of the black-footed ferret (Wisely 2006), which may explain why the species is able to survive and reproduce successfully despite low levels of genetic diversity. While the species appears to be tolerant of reduced genetic diversity, the long-term effects of reduced diversity are unknown, and could manifest themselves in a loss of ability to adapt to changing environments (Hoffman et al. 2003, Traill et al. 2010). Because many reintroduction sites are maintained through frequent augmentation with captive-reared animals, the reintroduced population remains virtually indistinguishable genetically from the captive population. Representation in the context of genetic diversity remains low, and frequent augmentation limits the cultural transmission of important behaviors in the reintroduced population (Biggins 2000).

Since all extant black-footed ferrets are descendants of seven founder animals, their genetic representation is understandably limited. In our future condition analysis, we projected genetic representation will not change for the captive population, with the exception of the Optimistic and Transformation Scenarios, where incorporation of new genetic material was introduced as a possibility. Similarly, we projected that genetic representation will not change for the reintroduced population, although it is possible that long-term reintroduction sites such as Conata Basin-Badlands, South Dakota, and Shirley Basin, Wyoming may differentiate themselves genetically during longer timeframes under the Optimistic and Transformation Scenarios.

Ecological representation in our future condition analysis did not change appreciably with respect to the reintroduced population, as active sites were maintained within the habitat of all three species of prairie dogs, with the exception of the Disastrous Scenario in 2039. This is likely the effect of changing climate reducing the resiliency of Gunnison's prairie dog reintroduction sites in the southern portion of the black-footed ferret's potential range.

5.4 Synopsis of Viability

The black-footed ferret currently exhibits moderate to low levels of resiliency, redundancy, and representation, which are maintained with the assistance of significant management inputs. The viability of both populations is dependent on the continued availability of resources for management, which in the case of the reintroduced population are diminished in effectiveness due to climate change, and in the case of both populations may be diminished due to declining genetic fitness. Importantly, a continuation of current conditions into the future is projected to lead to a decline in overall condition for most analysis units in both populations, underscoring the need to maintain and improve upon management inputs to retain current levels of viability. Management inputs will need to be refined and expanded in scope in order to overcome the challenges of decreasing genetic diversity, sylvatic plague, and lack of suitable habitat to increase the overall viability of the black-footed ferret.

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Appendix – Future Condition Tables

Appendix Table 1. Future condition table for facilities housing the captive black-footed ferret population, continuation scenario, 10 years into the future. Numbers denote resiliency class scores (1=low, 2=moderate, and 3=high).

Facility	% Whelping success	Mean # kits/litter	% Kits weaned	TOTAL SCORE
National Black-footed Ferret Conservation Center	1	3	2	**6**
Smithsonian Conservation Biology Institute	3	3	2	**8**
Louisville Zoological Garden	2	2	1	**5**
Cheyenne Mountain Zoo	1	3	1	**5**
Phoenix Zoo	1	1	1	**3**
Toronto Zoo	1	2	2	**5**

Appendix Table 2. Future condition table for facilities housing the captive black-footed ferret population, continuation scenario, 20 years into the future. Numbers denote resiliency class scores (1=low, 2=moderate, and 3=high).

Facility	% Whelping success	Mean # kits/litter	% Kits weaned	TOTAL SCORE
National Black-footed Ferret Conservation Center	1	3	2	**6**
Smithsonian Conservation Biology Institute	2	3	2	**7**
Louisville Zoological Garden	2	1	1	**4**
Cheyenne Mountain Zoo	1	3	1	**5**
Phoenix Zoo	1	1	1	**3**
Toronto Zoo	1	1	2	**4**

Appendix Table 3. Future condition table for 29 black-footed ferret reintroduction sites, continuation scenario, 10 years into the future. Numbers denote resiliency class scores (0=inactive, 1=low, 2=moderate, and 3=high).

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Conata Basin, SD	BTPD	3	3	3	3	3	3	18	1	69
UL Bend NWR, MT	BTPD	1	1	2	3	2	3	12	1	33
Ft. Belknap, MT	BTPD	1	1	2	3	1	2	10	1	31
Cheyenne River, SD	BTPD	1	2	1	1	1	1	7	0	0
BLM 40 Complex, MT	BTPD	0	1	1	1	0	1	4	0	0
Janos, MX	BTPD	0	2	1	1	0	1	5	0	0
Rosebud, SD	BTPD	1	2	1	1	1	1	7	0	0
Lower Brule, SD	BTPD	1	1	2	3	1	2	11	1	31
Wind Cave NP, SD	BTPD	1	2	2	3	1	3	12	1	37
Butte Creek Ranches, KS	BTPD	1	2	2	3	1	3	12	1	37
Northern Cheyenne, MT	BTPD	0	1	1	1	0	1	4	0	0
Vermejo BTPD, NM	BTPD	1	2	1	1	1	3	9	0	0
Grasslands NP, SK	BTPD	0	1	1	1	0	3	6	0	0
Walker Ranch, CO	BTPD	0	1	3	1	0	3	8	0	0
City of Fort Collins, CO	BTPD	1	1	3	3	1	3	12	1	37
North Holly, CO	BTPD	1	1	3	1	1	3	10	0	0
Liberty, CO	BTPD	1	1	3	1	1	3	10	0	0
Rocky Mountain Arsenal NWR, CO	BTPD	2	2	3	3	3	3	16	1	54
Crow Reservation, MT	BTPD	1	1	2	2	1	2	9	1	30
South Holly, CO	BTPD	1	1	3	1	1	3	10	0	0
Bad River Ranch, SD	BTPD	1	1	2	1	1	3	9	0	0

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Moore Ranch, NM	BTPD	1	1	3	1	1	3	10	0	0
Aubrey Valley, AZ	GPD	2	2	2	2	1	2	11	1	45
Espee Ranch, AZ	GPD	1	2	2	1	1	2	9	0	0
Vermejo GPD, NM	GPD	1	1	1	1	1	3	8	0	0
Shirley Basin, WY	WTPD	2	3	1	2	2	2	11	1	46
Coyote Basin, CO-UT	WTPD	1	3	2	1	1	2	10	1	39
Wolf Creek, CO	WTPD	0	1	1	1	0	2	5	0	0
Meeteetse, WY	WTPD	1	2	3	3	1	2	12	0	41

***Adjusted Current Condition** is a weighted value that is the result of multiplying the 5-year mean # of breeding adults condition class by 10 and the 5-year mean ferret family rating and annual plague management level condition classes by 5, and adding these values to the remaining condition classes. **Condition class rankings are as follows: 0 = Inactive, ≤ 33 = Low, > 33 and ≤ 50 = Moderate, > 50 = High**

Appendix Table 4. Future condition table for 29 black-footed ferret reintroduction sites, continuation scenario, 20 years into the future. Numbers denote resiliency class scores (0=inactive, 1=low, 2=moderate, and 3=high).

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Conata Basin, SD	BTPD	3	3	3	3	3	3	18	1	69
UL Bend NWR, MT	BTPD	1	1	2	3	2	3	12	1	33
Ft. Belknap, MT	BTPD	1	1	2	3	1	2	10	1	31
Cheyenne River, SD	BTPD	1	2	1	1	1	1	7	0	0
BLM 40 Complex, MT	BTPD	0	1	1	1	0	1	4	0	0
Janos, MX	BTPD	0	2	1	1	0	1	5	0	0
Rosebud, SD	BTPD	1	2	1	1	1	1	7	0	0
Lower Brule, SD	BTPD	1	1	2	3	1	2	11	1	31
Wind Cave NP, SD	BTPD	1	2	2	3	1	3	12	1	37
Butte Creek Ranches, KS	BTPD	1	2	2	3	1	3	12	1	37
Northern Cheyenne, MT	BTPD	0	1	1	1	0	1	4	0	0
Vermejo BTPD, NM	BTPD	1	2	1	1	1	3	9	0	0
Grasslands NP, SK	BTPD	0	1	1	1	0	3	6	0	0
Walker Ranch, CO	BTPD	0	1	3	1	0	3	8	0	0
City of Fort Collins, CO	BTPD	1	1	3	3	1	3	12	1	37
North Holly, CO	BTPD	1	1	3	1	1	3	10	0	0
Liberty, CO	BTPD	1	1	3	1	1	3	10	0	0
Rocky Mountain Arsenal NWR, CO	BTPD	2	2	3	3	3	3	16	1	54
Crow Reservation, MT	BTPD	1	1	2	2	1	2	9	0	0
South Holly, CO	BTPD	1	1	3	1	1	3	10	0	0
Bad River Ranch, SD	BTPD	1	1	2	1	1	3	9	0	0

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Moore Ranch, NM	BTPD	1	1	3	1	1	3	10	0	0
Aubrey Valley, AZ	GPD	2	2	2	2	1	2	11	1	45
Espee Ranch, AZ	GPD	1	2	2	1	1	2	9	0	0
Vermejo GPD, NM	GPD	1	1	1	1	1	3	8	0	0
Shirley Basin, WY	WTPD	2	3	1	2	2	2	11	1	46
Coyote Basin, CO-UT	WTPD	1	2	2	1	1	2	9	1	33
Wolf Creek, CO	WTPD	0	1	1	1	0	2	5	0	0
Meeteetse, WY	WTPD	1	2	3	3	1	2	12	0	41

*__Adjusted Current Condition__ is a weighted value that is the result of multiplying the 5-year mean # of breeding adults condition class by 10 and the 5-year mean ferret family rating and annual plague management level condition classes by 5, and adding these values to the remaining condition classes. **Condition class rankings are as follows: 0 = Inactive, ≤ 33 = Low, > 33 and ≤ 50 = Moderate, > 50 = High**

Appendix Table 5. Future condition table for facilities housing the captive black-footed ferret population, pessimistic scenario, 10 years into the future. Numbers denote resiliency class scores (1=low, 2=moderate, and 3=high).

Facility	% Whelping success	Mean # kits/litter	% Kits weaned	TOTAL SCORE
National Black-footed Ferret Conservation Center	1	2	1	**4**
Smithsonian Conservation Biology Institute	2	2	1	**5**
Louisville Zoological Garden	2	2	1	**5**
Cheyenne Mountain Zoo	1	2	1	**4**
Phoenix Zoo	1	1	1	**3**
Toronto Zoo	1	2	1	**4**

Appendix Table 6. Future condition table for facilities housing the captive black-footed ferret population, pessimistic scenario, 20 years into the future. Numbers denote resiliency class scores (1=low, 2=moderate, and 3=high).

Facility	% Whelping success	Mean # kits/litter	% Kits weaned	TOTAL SCORE
National Black-footed Ferret Conservation Center	1	2	1	**4**
Smithsonian Conservation Biology Institute	2	2	1	**5**
Louisville Zoological Garden	2	1	1	**4**
Cheyenne Mountain Zoo	1	2	1	**4**
Phoenix Zoo	1	1	1	**3**
Toronto Zoo	1	2	1	**4**

Appendix Table 7. Future condition table for 29 black-footed ferret reintroduction sites, pessimistic scenario, 10 years into the future. Numbers denote resiliency class scores (0=inactive, 1=low, 2=moderate, and 3=high).

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Conata Basin, SD	BTPD	2	2	2	2	3	3	14	1	48
UL Bend NWR, MT	BTPD	1	1	1	2	0	3	9	0	0
Ft. Belknap, MT	BTPD	1	1	1	2	0	2	7	0	0
Cheyenne River, SD	BTPD	1	2	1	1	1	1	7	0	0
BLM 40 Complex, MT	BTPD	0	1	1	1	0	1	4	0	0
Janos, MX	BTPD	0	2	1	1	0	1	5	0	0
Rosebud, SD	BTPD	1	2	1	1	1	1	7	0	0
Lower Brule, SD	BTPD	1	1	2	2	1	2	9	1	30
Wind Cave NP, SD	BTPD	1	1	2	2	1	3	10	1	31
Butte Creek Ranches, KS	BTPD	1	1	2	2	1	3	10	1	31
Northern Cheyenne, MT	BTPD	0	1	1	1	0	1	4	0	0
Vermejo BTPD, NM	BTPD	1	2	1	1	1	3	9	0	0
Grasslands NP, SK	BTPD	0	1	1	1	0	3	6	0	0
Walker Ranch, CO	BTPD	0	1	2	1	0	3	7	0	0
City of Fort Collins, CO	BTPD	1	1	2	2	1	3	10	1	31
North Holly, CO	BTPD	1	1	2	1	1	3	9	0	0
Liberty, CO	BTPD	1	1	2	1	1	3	9	0	0
Rocky Mountain Arsenal NWR, CO	BTPD	2	2	2	2	2	3	14	1	47
Crow Reservation, MT	BTPD	1	1	1	1	1	2	7	0	0
South Holly, CO	BTPD	1	1	2	1	1	3	9	0	0
Bad River Ranch, SD	BTPD	1	1	2	1	1	3	9	0	0

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Moore Ranch, NM	BTPD	1	1	2	1	1	3	9	0	0
Aubrey Valley, AZ	GPD	2	2	1	2	1	2	10	1	36
Espee Ranch, AZ	GPD	1	1	1	1	1	2	7	0	0
Vermejo GPD, NM	GPD	1	1	1	1	1	3	8	0	0
Shirley Basin, WY	WTPD	2	2	1	2	2	2	11	1	37
Coyote Basin, CO-UT	WTPD	1	2	1	1	1	2	8	1	29
Wolf Creek, CO	WTPD	0	1	1	1	0	2	5	0	0
Meeteetse, WY	WTPD	1	2	2	2	1	2	10	0	35

*__Adjusted Current Condition__ is a weighted value that is the result of multiplying the 5-year mean # of breeding adults condition class by 10 and the 5-year mean ferret family rating and annual plague management level condition classes by 5, and adding these values to the remaining condition classes. **Condition class rankings are as follows: 0 = Inactive, ≤ 33 = Low, > 33 and ≤ 50 = Moderate, > 50 = High**

Appendix Table 8. Future condition table for 29 black-footed ferret reintroduction sites, pessimistic scenario, 20 years into the future. Numbers denote resiliency class scores (0=inactive, 1=low, 2=moderate, and 3=high).

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Conata Basin, SD	BTPD	2	2	2	2	3	3	14	1	48
UL Bend NWR, MT	BTPD	1	1	1	2	0	3	9	0	0
Ft. Belknap, MT	BTPD	1	1	1	2	0	2	7	0	0
Cheyenne River, SD	BTPD	1	2	1	1	1	1	7	0	0
BLM 40 Complex, MT	BTPD	0	1	1	1	0	1	4	0	0
Janos, MX	BTPD	0	2	1	1	0	1	5	0	0
Rosebud, SD	BTPD	1	2	1	1	1	1	7	0	0
Lower Brule, SD	BTPD	1	1	2	2	1	2	9	1	30
Wind Cave NP, SD	BTPD	1	1	2	2	1	3	10	1	31
Butte Creek Ranches, KS	BTPD	1	1	2	2	1	3	10	1	31
Northern Cheyenne, MT	BTPD	0	1	1	1	0	1	4	0	0
Vermejo BTPD, NM	BTPD	1	2	1	1	1	3	9	0	0
Grasslands NP, SK	BTPD	0	1	1	1	0	3	6	0	0
Walker Ranch, CO	BTPD	0	1	2	1	0	3	7	0	0
City of Fort Collins, CO	BTPD	1	1	2	2	1	3	10	1	31
North Holly, CO	BTPD	1	1	2	1	1	3	9	0	0
Liberty, CO	BTPD	1	1	2	1	1	3	9	0	0
Rocky Mountain Arsenal NWR, CO	BTPD	2	2	2	2	2	3	14	1	47
Crow Reservation, MT	BTPD	1	1	1	1	1	2	7	0	0
South Holly, CO	BTPD	1	1	2	1	1	3	9	0	0
Bad River Ranch, SD	BTPD	1	1	2	1	1	3	9	0	0

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Moore Ranch, NM	BTPD	1	1	2	1	1	3	9	0	0
Aubrey Valley, AZ	GPD	2	1	1	2	1	2	9	1	35
Espee Ranch, AZ	GPD	1	1	1	1	1	2	7	0	0
Vermejo GPD, NM	GPD	1	1	1	1	1	3	8	0	0
Shirley Basin, WY	WTPD	2	2	1	2	2	2	11	1	41
Coyote Basin, CO-UT	WTPD	1	1	1	1	1	2	7	1	24
Wolf Creek, CO	WTPD	0	1	1	1	0	2	5	0	0
Meeteetse, WY	WTPD	1	2	2	2	1	2	10	0	35

***Adjusted Current Condition** is a weighted value that is the result of multiplying the 5-year mean # of breeding adults condition class by 10 and the 5-year mean ferret family rating and annual plague management level condition classes by 5, and adding these values to the remaining condition classes. **Condition class rankings are as follows: 0 = Inactive, ≤ 33 = Low, > 33 and ≤ 50 = Moderate, > 50 = High**

Appendix Table 9. Future condition table for facilities housing the captive black-footed ferret population, disastrous scenario, 10 years into the future. Numbers denote resiliency class scores (1=low, 2=moderate, and 3=high).

Facility	% Whelping success	Mean # kits/litter	% Kits weaned	TOTAL SCORE
National Black-footed Ferret Conservation Center	1	1	1	**3**
Smithsonian Conservation Biology Institute	1	1	1	**3**
Louisville Zoological Garden	1	1	1	**3**
Cheyenne Mountain Zoo	1	1	1	**3**
Phoenix Zoo	1	1	1	**3**
Toronto Zoo	1	1	1	**3**

Appendix Table 10. Future condition table for facilities housing the captive black-footed ferret population, disastrous scenario, 20 years into the future. Numbers denote resiliency class scores (1=low, 2=moderate, and 3=high).

Facility	% Whelping success	Mean # kits/litter	% Kits weaned	TOTAL SCORE
National Black-footed Ferret Conservation Center	1	1	1	**3**
Smithsonian Conservation Biology Institute	1	1	1	**3**
Louisville Zoological Garden	1	1	1	**3**
Cheyenne Mountain Zoo	1	1	1	**3**
Phoenix Zoo	1	1	1	**3**
Toronto Zoo	1	1	1	**3**

Appendix Table 11. Future condition table for 29 black-footed ferret reintroduction sites, disastrous scenario, 10 years into the future. Numbers denote resiliency class scores (0=inactive, 1=low, 2=moderate, and 3=high).

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Conata Basin, SD	BTPD	2	2	1	1	3	2	11	1	41
UL Bend NWR, MT	BTPD	1	1	1	1	1	3	8	0	0
Ft. Belknap, MT	BTPD	1	1	1	1	1	1	6	0	0
Cheyenne River, SD	BTPD	1	1	1	1	1	1	6	0	0
BLM 40 Complex, MT	BTPD	0	1	1	1	0	1	4	0	0
Janos, MX	BTPD	0	1	1	1	0	1	4	0	0
Rosebud, SD	BTPD	1	1	1	1	1	1	6	0	0
Lower Brule, SD	BTPD	1	1	1	1	1	1	6	0	0
Wind Cave NP, SD	BTPD	1	1	1	1	1	3	8	0	0
Butte Creek Ranches, KS	BTPD	1	1	1	1	1	3	8	0	0
Northern Cheyenne, MT	BTPD	0	1	1	1	0	1	4	0	0
Vermejo BTPD, NM	BTPD	1	1	1	1	1	1	6	0	0
Grasslands NP, SK	BTPD	0	1	1	1	0	3	6	0	0
Walker Ranch, CO	BTPD	0	1	1	1	0	1	7	0	0
City of Fort Collins, CO	BTPD	1	1	1	1	1	1	6	0	0
North Holly, CO	BTPD	1	1	1	1	1	1	6	0	0
Liberty, CO	BTPD	1	1	1	1	1	1	6	0	0
Rocky Mountain Arsenal NWR, CO	BTPD	2	2	1	1	2	3	11	1	41
Crow Reservation, MT	BTPD	1	1	1	1	1	1	6	0	0
South Holly, CO	BTPD	1	1	1	1	1	1	6	0	0
Bad River Ranch, SD	BTPD	1	1	1	1	1	1	6	0	0

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Moore Ranch, NM	BTPD	1	1	1	1	1	1	6	0	0
Aubrey Valley, AZ	GPD	1	1	1	1	1	1	6	0	0
Espee Ranch, AZ	GPD	1	1	1	1	1	1	6	0	0
Vermejo GPD, NM	GPD	1	1	1	1	1	1	6	0	0
Shirley Basin, WY	WTPD	2	2	1	1	2	1	9	1	35
Coyote Basin, CO-UT	WTPD	1	1	1	1	1	1	6	0	0
Wolf Creek, CO	WTPD	0	1	1	1	0	1	4	0	0
Meeteetse, WY	WTPD	1	1	1	1	1	1	6	1	23

***Adjusted Current Condition** is a weighted value that is the result of multiplying the 5-year mean # of breeding adults condition class by 10 and the 5-year mean ferret family rating and annual plague management level condition classes by 5, and adding these values to the remaining condition classes. **Condition class rankings are as follows: 0 = Inactive, ≤ 33 = Low, > 33 and ≤ 50 = Moderate, > 50 = High**

Appendix Table 12. Future condition table for 29 black-footed ferret reintroduction sites, disastrous scenario, 20 years into the future. Numbers denote resiliency class scores (0=inactive, 1=low, 2=moderate, and 3=high).

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Conata Basin, SD	BTPD	2	2	1	1	3	2	11	1	41
UL Bend NWR, MT	BTPD	1	1	1	1	1	3	8	0	0
Ft. Belknap, MT	BTPD	1	1	1	1	1	1	6	0	0
Cheyenne River, SD	BTPD	1	1	1	1	1	1	6	0	0
BLM 40 Complex, MT	BTPD	0	1	1	1	0	1	4	0	0
Janos, MX	BTPD	0	1	1	1	0	1	4	0	0
Rosebud, SD	BTPD	1	1	1	1	1	1	6	0	0
Lower Brule, SD	BTPD	1	1	1	1	1	1	6	0	0
Wind Cave NP, SD	BTPD	1	1	1	1	1	3	8	0	0
Butte Creek Ranches, KS	BTPD	1	1	1	1	1	3	8	0	0
Northern Cheyenne, MT	BTPD	0	1	1	1	0	1	4	0	0
Vermejo BTPD, NM	BTPD	1	1	1	1	1	1	6	0	0
Grasslands NP, SK	BTPD	0	1	1	1	0	3	6	0	0
Walker Ranch, CO	BTPD	0	1	1	1	0	1	7	0	0
City of Fort Collins, CO	BTPD	1	1	1	1	1	1	6	0	0
North Holly, CO	BTPD	1	1	1	1	1	1	6	0	0
Liberty, CO	BTPD	1	1	1	1	1	1	6	0	0
Rocky Mountain Arsenal NWR, CO	BTPD	2	2	1	1	2	3	11	1	41
Crow Reservation, MT	BTPD	1	1	1	1	1	1	6	0	0
South Holly, CO	BTPD	1	1	1	1	1	1	6	0	0
Bad River Ranch, SD	BTPD	1	1	1	1	1	1	6	0	0

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Moore Ranch, NM	BTPD	1	1	1	1	1	1	6	0	0
Aubrey Valley, AZ	GPD	1	1	1	1	1	1	6	0	0
Espee Ranch, AZ	GPD	1	1	1	1	1	1	6	0	0
Vermejo GPD, NM	GPD	1	1	1	1	1	1	6	0	0
Shirley Basin, WY	WTPD	2	2	1	1	2	1	9	1	35
Coyote Basin, CO-UT	WTPD	1	1	1	1	1	1	6	0	0
Wolf Creek, CO	WTPD	0	1	1	1	0	1	4	0	0
Meeteetse, WY	WTPD	1	1	1	1	1	1	6	0	0

***Adjusted Current Condition** is a weighted value that is the result of multiplying the 5-year mean # of breeding adults condition class by 10 and the 5-year mean ferret family rating and annual plague management level condition classes by 5, and adding these values to the remaining condition classes. **Condition class rankings are as follows: 0 = Inactive, ≤ 33 = Low, > 33 and ≤ 50 = Moderate, > 50 = High**

Appendix Table 13. Future condition table for facilities housing the captive black-footed ferret population, optimistic scenario, 10 years into the future. Numbers denote resiliency class scores (1=low, 2=moderate, and 3=high).

Facility	% Whelping success	Mean # kits/litter	% Kits weaned	TOTAL SCORE
National Black-footed Ferret Conservation Center	2	3	3	**8**
Smithsonian Conservation Biology Institute	3	3	3	**9**
Louisville Zoological Garden	3	3	2	**8**
Cheyenne Mountain Zoo	2	3	3	**8**
Phoenix Zoo	2	2	1	**5**
Toronto Zoo	2	3	3	**8**

Appendix Table 14. Future condition table for facilities housing the captive black-footed ferret population, optimistic scenario, 20 years into the future. Numbers denote resiliency class scores (1=low, 2=moderate, and 3=high).

Facility	% Whelping success	Mean # kits/litter	% Kits weaned	TOTAL SCORE
National Black-footed Ferret Conservation Center	3	3	3	**9**
Smithsonian Conservation Biology Institute	3	3	3	**9**
Louisville Zoological Garden	3	3	2	**8**
Cheyenne Mountain Zoo	2	3	3	**8**
Phoenix Zoo	2	2	2	**6**
Toronto Zoo	2	3	3	**8**

Appendix Table 15. Future condition table for 29 black-footed ferret reintroduction sites, optimistic scenario, 10 years into the future. Numbers denote resiliency class scores (0=inactive, 1=low, 2=moderate, and 3=high).

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Conata Basin, SD	BTPD	3	3	3	3	3	3	18	1	69
UL Bend NWR, MT	BTPD	2	2	3	3	2	3	15	1	53
Ft. Belknap, MT	BTPD	2	2	2	2	2	2	12	1	46
Cheyenne River, SD	BTPD	2	2	2	2	2	2	12	1	46
BLM 40 Complex, MT	BTPD	1	1	3	2	1	2	10	1	35
Janos, MX	BTPD	1	2	2	1	1	1	8	0	0
Rosebud, SD	BTPD	2	2	2	1	2	2	11	1	45
Lower Brule, SD	BTPD	1	1	3	3	2	2	12	1	37
Wind Cave NP, SD	BTPD	1	2	3	3	2	3	14	1	43
Butte Creek Ranches, KS	BTPD	2	2	3	3	2	3	15	1	53
Northern Cheyenne, MT	BTPD	1	1	2	1	1	1	7	1	28
Vermejo BTPD, NM	BTPD	2	2	2	1	1	3	11	1	45
Grasslands NP, SK	BTPD	1	1	3	2	1	3	11	1	36
Walker Ranch, CO	BTPD	1	1	3	1	1	3	10	1	35
City of Fort Collins, CO	BTPD	1	1	3	3	1	3	12	1	37
North Holly, CO	BTPD	1	1	3	1	1	3	10	0	0
Liberty, CO	BTPD	1	1	3	1	1	3	10	0	0
Rocky Mountain Arsenal NWR, CO	BTPD	2	2	3	3	3	3	16	1	54
Crow Reservation, MT	BTPD	1	1	2	2	1	2	9	1	30
South Holly, CO	BTPD	1	1	3	1	1	3	10	0	0
Bad River Ranch, SD	BTPD	1	1	2	1	1	3	9	1	30

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Moore Ranch, NM	BTPD	1	1	2	1	1	3	9	0	0
Aubrey Valley, AZ	GPD	3	2	3	2	2	2	14	1	61
Espee Ranch, AZ	GPD	1	2	2	2	1	2	10	1	35
Vermejo GPD, NM	GPD	1	1	1	1	1	3	8	0	0
Shirley Basin, WY	WTPD	2	3	2	2	2	2	13	1	51
Coyote Basin, CO-UT	WTPD	2	3	2	2	2	2	13	1	51
Wolf Creek, CO	WTPD	1	2	2	2	1	2	10	1	34
Meeteetse, WY	WTPD	2	2	3	3	2	2	14	0	52

*__Adjusted Current Condition__ is a weighted value that is the result of multiplying the 5-year mean # of breeding adults condition class by 10 and the 5-year mean ferret family rating and annual plague management level condition classes by 5, and adding these values to the remaining condition classes. **Condition class rankings are as follows: 0 = Inactive, ≤ 33 = Low, > 33 and ≤ 50 = Moderate, > 50 = High**

Appendix Table 16. Future condition table for 29 black-footed ferret reintroduction sites, optimistic scenario, 20 years into the future. Numbers denote resiliency class scores (0=inactive, 1=low, 2=moderate, and 3=high).

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Conata Basin, SD	BTPD	3	3	3	3	3	3	18	1	69
UL Bend NWR, MT	BTPD	2	2	3	3	2	3	15	1	53
Ft. Belknap, MT	BTPD	2	2	2	2	2	2	12	1	46
Cheyenne River, SD	BTPD	2	2	2	2	2	2	12	1	46
BLM 40 Complex, MT	BTPD	1	1	3	2	1	2	10	1	35
Janos, MX	BTPD	1	2	2	1	1	1	8	0	0
Rosebud, SD	BTPD	2	2	2	1	2	2	11	1	45
Lower Brule, SD	BTPD	1	1	3	3	2	2	12	1	37
Wind Cave NP, SD	BTPD	1	2	3	3	2	3	14	1	43
Butte Creek Ranches, KS	BTPD	2	2	3	3	2	3	15	1	53
Northern Cheyenne, MT	BTPD	1	1	2	1	1	1	7	1	28
Vermejo BTPD, NM	BTPD	2	1	2	1	1	3	10	1	30
Grasslands NP, SK	BTPD	1	1	3	2	1	3	11	1	36
Walker Ranch, CO	BTPD	1	1	3	1	1	3	10	1	35
City of Fort Collins, CO	BTPD	1	1	3	3	1	3	12	1	37
North Holly, CO	BTPD	1	1	3	1	1	3	10	0	0
Liberty, CO	BTPD	1	1	3	1	1	3	10	0	0
Rocky Mountain Arsenal NWR, CO	BTPD	2	2	3	3	3	3	16	1	54
Crow Reservation, MT	BTPD	1	1	2	2	1	2	9	1	30
South Holly, CO	BTPD	1	1	3	1	1	3	10	0	0
Bad River Ranch, SD	BTPD	1	1	2	1	1	3	9	1	30

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Moore Ranch, NM	BTPD	1	1	2	1	1	3	9	0	0
Aubrey Valley, AZ	GPD	2	2	3	2	2	2	13	1	51
Espee Ranch, AZ	GPD	1	1	2	2	1	2	9	1	30
Vermejo GPD, NM	GPD	1	1	1	1	1	3	8	0	0
Shirley Basin, WY	WTPD	2	3	2	2	2	2	13	1	51
Coyote Basin, CO-UT	WTPD	2	2	2	2	2	2	12	1	46
Wolf Creek, CO	WTPD	1	2	2	2	1	2	10	1	34
Meeteetse, WY	WTPD	2	2	3	3	2	2	14	0	52

***Adjusted Current Condition** is a weighted value that is the result of multiplying the 5-year mean # of breeding adults condition class by 10 and the 5-year mean ferret family rating and annual plague management level condition classes by 5, and adding these values to the remaining condition classes. **Condition class rankings are as follows: 0 = Inactive, ≤ 33 = Low, > 33 and ≤ 50 = Moderate, > 50 = High**

Appendix Table 17. Future condition table for facilities housing the captive black-footed ferret population, transformation scenario, 10 years into the future. Numbers denote resiliency class scores (1=low, 2=moderate, and 3=high).

Facility	% Whelping success	Mean # kits/litter	% Kits weaned	TOTAL SCORE
National Black-footed Ferret Conservation Center	3	3	3	**9**
Smithsonian Conservation Biology Institute	3	3	3	**9**
Louisville Zoological Garden	3	3	3	**9**
Cheyenne Mountain Zoo	3	3	3	**9**
Phoenix Zoo	3	3	3	**9**
Toronto Zoo	3	3	3	**9**

Appendix Table 18. Future condition table for facilities housing the captive black-footed ferret population, transformation scenario, 20 years into the future. Numbers denote resiliency class scores (1=low, 2=moderate, and 3=high).

Facility	% Whelping success	Mean # kits/litter	% Kits weaned	TOTAL SCORE
National Black-footed Ferret Conservation Center	3	3	3	**9**
Smithsonian Conservation Biology Institute	3	3	3	**9**
Louisville Zoological Garden	3	3	3	**9**
Cheyenne Mountain Zoo	3	3	3	**9**
Phoenix Zoo	3	3	3	**9**
Toronto Zoo	3	3	3	**9**

Appendix Table 19. Future condition table for 29 black-footed ferret reintroduction sites, transformation scenario, 10 years into the future. Numbers denote resiliency class scores (0=inactive, 1=low, 2=moderate, and 3=high).

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Conata Basin, SD	BTPD	3	3	3	3	3	3	18	1	69
UL Bend NWR, MT	BTPD	2	2	3	3	3	3	16	1	54
Ft. Belknap, MT	BTPD	3	3	3	3	3	3	18	1	69
Cheyenne River, SD	BTPD	3	3	3	3	3	3	18	1	69
BLM 40 Complex, MT	BTPD	1	2	3	3	3	3	15	1	44
Janos, MX	BTPD	3	3	3	3	3	3	18	1	69
Rosebud, SD	BTPD	3	3	3	3	3	3	18	1	69
Lower Brule, SD	BTPD	2	2	3	3	2	2	14	1	52
Wind Cave NP, SD	BTPD	2	2	3	3	3	3	16	1	54
Butte Creek Ranches, KS	BTPD	3	2	3	3	2	3	17	1	63
Northern Cheyenne, MT	BTPD	2	2	2	2	2	2	12	1	46
Vermejo BTPD, NM	BTPD	3	3	3	3	3	3	18	1	69
Grasslands NP, SK	BTPD	1	2	3	3	2	3	15	1	43
Walker Ranch, CO	BTPD	2	2	3	3	2	3	15	1	53
City of Fort Collins, CO	BTPD	1	2	3	3	3	3	15	1	44
North Holly, CO	BTPD	1	2	3	3	2	3	14	1	43
Liberty, CO	BTPD	1	2	3	3	2	3	14	1	43
Rocky Mountain Arsenal NWR, CO	BTPD	3	2	3	3	3	3	17	1	64
Crow Reservation, MT	BTPD	2	2	2	2	2	2	12	1	46
South Holly, CO	BTPD	1	1	3	3	1	3	12	1	37
Bad River Ranch, SD	BTPD	2	2	3	3	3	3	16	1	54

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Moore Ranch, NM	BTPD	1	1	3	3	1	3	12	1	37
Aubrey Valley, AZ	GPD	2	2	3	3	3	2	17	1	53
Espee Ranch, AZ	GPD	2	2	3	3	2	2	14	1	52
Vermejo GPD, NM	GPD	2	2	3	3	2	3	15	1	53
Shirley Basin, WY	WTPD	3	3	3	3	3	2	17	1	68
Coyote Basin, CO-UT	WTPD	2	2	3	3	3	2	17	1	53
Wolf Creek, CO	WTPD	2	2	3	3	2	2	15	1	52
Meeteetse, WY	WTPD	3	3	3	3	3	2	17	0	68

***Adjusted Current Condition** is a weighted value that is the result of multiplying the 5-year mean # of breeding adults condition class by 10 and the 5-year mean ferret family rating and annual plague management level condition classes by 5, and adding these values to the remaining condition classes. **Condition class rankings are as follows: 0 = Inactive, ≤ 33 = Low, > 33 and ≤ 50 = Moderate, > 50 = High**

Appendix Table 20. Future condition table for 29 black-footed ferret reintroduction sites, transformation scenario, 20 years into the future. Numbers denote resiliency class scores (0=inactive, 1=low, 2=moderate, and 3=high).

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Conata Basin, SD	BTPD	3	3	3	3	3	3	18	1	69
UL Bend NWR, MT	BTPD	2	2	3	3	3	3	16	1	54
Ft. Belknap, MT	BTPD	3	3	3	3	3	3	18	1	69
Cheyenne River, SD	BTPD	3	3	3	3	3	3	18	1	69
BLM 40 Complex, MT	BTPD	1	2	3	3	3	3	15	1	44
Janos, MX	BTPD	3	3	3	3	3	3	18	1	69
Rosebud, SD	BTPD	3	3	3	3	3	3	18	1	69
Lower Brule, SD	BTPD	2	2	3	3	2	2	14	1	52
Wind Cave NP, SD	BTPD	2	2	3	3	3	3	16	1	54
Butte Creek Ranches, KS	BTPD	3	2	3	3	2	3	17	1	63
Northern Cheyenne, MT	BTPD	2	2	2	2	2	2	12	1	46
Vermejo BTPD, NM	BTPD	3	3	3	3	3	3	18	1	69
Grasslands NP, SK	BTPD	1	2	3	3	2	3	15	1	43
Walker Ranch, CO	BTPD	2	2	3	3	2	3	15	1	53
City of Fort Collins, CO	BTPD	1	2	3	3	3	3	15	1	44
North Holly, CO	BTPD	1	2	3	3	2	3	14	1	43
Liberty, CO	BTPD	1	2	3	3	2	3	14	1	43
Rocky Mountain Arsenal NWR, CO	BTPD	3	2	3	3	3	3	17	1	64
Crow Reservation, MT	BTPD	2	2	2	2	2	2	12	1	46
South Holly, CO	BTPD	1	1	3	3	1	3	12	1	37
Bad River Ranch, SD	BTPD	2	2	3	3	3	3	16	1	54

Site and Location	Prairie Dog Species	5-year mean # of breeding adults	5-year mean ferret family rating	Annual Plague Management Level	Annual Ferret Vaccination Level	Ferret Population Persistence	Level of PD Population Protection	Current Resiliency (Subtotal)	Occupancy Multiplier (1 or 0)	Adjusted Current Condition (weighted)*
Moore Ranch, NM	BTPD	1	1	3	3	1	3	12	1	37
Aubrey Valley, AZ	GPD	3	3	3	3	3	2	17	1	68
Espee Ranch, AZ	GPD	2	2	3	3	2	2	14	1	52
Vermejo GPD, NM	GPD	2	2	3	3	2	3	15	1	53
Shirley Basin, WY	WTPD	3	3	3	3	3	2	17	1	68
Coyote Basin, CO-UT	WTPD	3	3	3	3	3	2	17	1	68
Wolf Creek, CO	WTPD	2	3	3	3	2	2	15	1	57
Meeteetse, WY	WTPD	3	3	3	3	3	2	17	0	68

*__Adjusted Current Condition__ is a weighted value that is the result of multiplying the 5-year mean # of breeding adults condition class by 10 and the 5-year mean ferret family rating and annual plague management level condition classes by 5, and adding these values to the remaining condition classes. **Condition class rankings are as follows: 0 = Inactive, ≤ 33 = Low, > 33 and ≤ 50 = Moderate, > 50 = High**